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INFLUENCE OF CONTROLLABLE ENVIRONMENTAL CONDITIONS ON REGENERATION OF JACK PINE AND BLACK SPRUCE [1]

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INTRODUCTION

Jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) are important pulpwood species in the northern Lake States. Knowledge of conditions under which they can be successfully reproduced is essential to their forest management. An experiment was therefore undertaken to test the influences of those environmental conditions which seemed most important in relation to natural reproduction of these species. The influences studied were those of (1) density of tree cover, (2) density of lower ground cover, (3) character of soil surface, and (4) seed-destroying rodents and birds. These are all factors over which man can exercise some control.

In interpreting the results of this experiment, it must be borne in mind that they apply particularly to the shallow soils and relatively cool climate of northeastern Minnesota. Although black spruce occurs both in swamps and on upland, the results pertain only to upland.

REVIEW OF LITERATURE

Many investigations have been made on factors influencing the germination, survival, and growth of conifer seedlings. These studies have in almost all cases dealt with species other than jack pine and black spruce, but they have established several principles that are generally applicable.

Several investigators have shown that soil surface material has a decided influence upon germination and survival of young seedlings. Larsen (*8*)[4] sowed seed of western white pine (*Pinus monticola*) on several kinds of soil surface, including natural duff, ashes, partly burned duff, and freshly loosened soil from which the duff and humus layers had been raked. Germination was decidedly better on the bare loose soil, ashes, and partly burned duff than on the undisturbed duff. The poorer germination on duff as compared with bare soil or ashes was attributed to less favorable moisture conditions. Studies reported by Barr (*1*), Lowdermilk (*12*), Moore (*14*), Shirley (*20*), Griffith (*4*), Robertson,[5] Obsorne and Harper (*15*), and LeBarron and

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[3] Maintained by the U. S. Department of Agriculture at University Farm, St. Paul, Minn., in cooperation with the University of Minnesota.

[4] Italic numbers in parentheses refer to Literature Cited, p. 118.

[5] ROBERTSON, W. M. SOME REGENERATION PROBLEMS AT THE PETAWAWA FOREST EXPERIMENT STATION. Canada Dept. Int., Forest Serv. Res. Note 41, 32 pp., illus. 1935. [Processed.]

Eyre (*10*) have shown that the surface of the undisturbed forest floor is a poor medium for germination of conifer seeds as compared with exposed mineral soil. Barr showed that seed of Engelmann spruce (*Picea engelmanni*) would germinate freely on humus if watered daily.

Moore (*13*) and Barr (*1*) pointed out that humus differs greatly from mineral soil in moisture-holding properties. Moore (*14*) reported greater seedling mortality on duff than on mineral soil and attributed it in part to insufficiency of moisture which he believed may have resulted from the heavy drain by the mat of plant roots within the humus. According to Barr, drought mortality was no greater on humus than on a mineral soil. Haig (*5*) reported that drought losses were about the same on duff and mineral soil.

Larsen (*8*) observed that seedlings on ashes and mineral soil were taller and sturdier than those on unburned duff in northern Idaho. Moore (*13*) reported more rapid growth of seedlings on well-decomposed humus than on raw humus or mineral soil. Haig (*5*) found better growth on burnt mineral soil than on duff or natural mineral soil.

Heat injury caused by insolation has been shown by Haig (*5*) and Isaac (*6*) to be a major cause of seedling mortality. Haig, working with western white pine and associated trees, found that in full sunlight the surface of duff becomes much hotter than the surface of mineral soil, particularly during May and June, when new tree seedlings are still small and tender. Isaac found that in hot weather in the Pacific Northwest the daily maximum temperatures of an unshaded fire-blackened surface were considerably higher than those of comparable natural-colored mineral soils.

With regard to influence of plant cover on conifer reproduction, Toumey and Neethling (*22*), Haig (*5*), and Isaac (*6*) found that shade reduces or prevents mortality from excessive heat of the surface soil. On the other hand, plant cover competes with the reproduction for soil moisture. Toumey and Kienholz (*23*) demonstrated that trenching of small plots under forest cover is followed by remarkable increases in low vegetation. Korstian and Coile (*7*) determined that during periods of critical dryness significantly greater moisture was available on trenched plots than on adjacent untrenched plots. Shirley (*21*) found that during dry periods soil moisture became critically low more frequently on untrenched than on trenched quadrats. Haig's (*5*) studies with seedlings under tree cover of various densities showed that drought losses were more severe under heavy forest cover than where tree cover was light or lacking. Pearson (*17*), working with ponderosa pine (*Pinus ponderosa*) in the Southwest, concluded that moisture and light relations could not entirely account for the failure of reproduction under trees, and suggested that temperature or some other factor might play a part in it. Shirley (*18*) pointed out that light intensity is usually a governing factor in the growth of vegetation under a forest canpoy, and that (*19*) an understory of shrubs reduces light intensity much more than an overstory of old-growth red pine (*P. resinosa*). Shade, by restricting the rise of soil temperature, may retard the seasonal beginning of germination, according to Haig (*5*). Several workers, including Wahlenberg (*27*), Moore (*14*), and Shirley (*20*), have observed that falling leaves may smother small seedlings.

Destruction of seeds and seedlings by birds and rodents is sometimes a restrictive factor in the establishment of conifer reproduction (*27, 3*).[6] Insects, also, may be a cause of loss, as reported by Wahlenberg (*27*), Pearson (*16*), and Haig (*5*). Barr (*1*), who grouped bird and insect losses together, observed severe losses of this kind.

Losses of conifer seedlings by disease have been reported in connection with several studies of seedling establishment (*1, 27, 16, 5*). Pearson observed that damping-off losses were less in sunny than in shady locations. Haig's experiments failed to show consistent differences in damping-off losses between full-sun, part-shade, and full-shade stations; the losses were distinctly greater on duff than on mineral soil except under full shade. Barr found that losses from fungi were much higher on humus than on clay soil.

EXPERIMENTAL AREA

The site chosen for the experiment is an almost level upland, typically occupied by jack pine and black spruce, on the Superior National Forest near Ely, Minn. The locality is characterized by a cool and relatively short growing season. The length of the frost-free period averages 108 days (*24*) at Virginia, Minn., about 45 miles distant but nearest of the long-time weather stations. Annual precipitation at the same place averages only 26.54 inches (*25*), but is favorably distributed in relation to the summer period. In the 46 years 1894–1939, monthly precipitation totals during the growing season averaged as follows:

	Inches
May	2. 80
June	4. 05
July	3. 84
August	3. 61
September	3. 71

The soil, of glacial origin, covers the igneous bedrock (gabbro) to a depth of from 18 inches to 3 feet. It varies greatly in texture. Mechanical analysis of samples taken about 3 inches below the humus layer within the zone of seedling roots showed it to contain 18.9 percent of gravel-sized material. The finer portion was 65.0 percent sand, 25.0 percent silt, 2.8 percent clay, and 7.2 percent fine clay. Although individual samples had a considerable range, the soil may be described in general terms as a sandy loam. Its pH value, as determined by the colorimetric method with a LaMotte-Kenney soil-testing kit, was 5.2.

At the time the experiments were inaugurated the timber was 65 to 70 years old. The dominant jack pines averaged about 65 feet in height, which indicates the site to be of medium quality for the species (*26*). The timbered area consisted of two separate blocks, approximately one-half mile apart. On block I jack pine predominated, making up 62 percent of the basal area of the stand, and was followed by black spruce, 16 percent; quaking aspen (*Populus tremuloides*), 20 percent; and paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and eastern white pine (*Pinus strobus*), 2 percent. On block II black spruce was most prominent, amounting to 42

[6] BURLEIGH, T. D. THE RELATION OF BIRDS TO THE ESTABLISHMENT OF LONG-LEAF PINE SEEDLINGS IN SOUTHERN MISSISSIPPI. U. S. Forest Serv., South. Forest Expt. Sta. Occas. Paper 75, 5 pp., illus. 1938. [Processed.]

percent of the basal area of the stand. Jack pine composed 24 percent and quaking aspen 18 percent; the remaining 16 percent was paper birch, balsam fir, eastern white pine, and red pine.

The few shrubs present in the understory, principally American green alder (*Alnus crispa*) and two kinds of blueberry (*Vaccinium angustifolium laevifolium* and *V. canadense*), were small and suppressed. The herbaceous cover differed considerably on the two blocks in both abundance and kind. On block I the principal species were *Aster macrophyllus*, *Cornus canadensis*, *Maianthemum canadense*, and *Rubus pubescens*. The foliage of the herbaceous plants covered half or more of the ground surface, at least during early summer. On block II *C. canadensis* was by far the most common herbaceous flowering plant and there was a scattering of *Aralia nudicaulis*, *R. pubescens*, *Carex* spp., and *Agrostis hiemalis*, but altogether the flowering plants did not cover more than 5 or 10 percent of the ground surface. A hypnum moss, *Calliergon schreberi*, formed an almost continuous carpet over the forest floor on this block.

EXPERIMENTAL DESIGN AND PROCEDURE

The design of the experiment was a split-plot arrangement (*28*). On each of the two timbered blocks 1½ acres were clear cut and an equal area was thinned to 50 percent of the basal area. After the thinning, the light intensity under the tree canopy amounted to 43 percent of full sunlight, according to paired black and white Livingston atmometer spheres 8 inches above the ground surface. In the center of each of the two clear-cut plots and the two thinned plots an area 32 feet by 36 feet was fenced against deer and rabbits. These four areas were designated for detailed seed-sowing tests. As natural seeding of all the experimental plots would be too uncertain and would in any case take too long a time, seed was sown artificially, in a manner resembling natural seeding. The enclosed plots were further subdivided, as shown diagrammatically in figure 1, to bring out the reactions to different factors affecting germination, survival, and growth of reproduction. Specifically, the experiment was designed to answer questions as to the influences of:

1. Density of tree cover:
   a. Half of full density
   b. None
2. Density of lower cover (shrubs and herbs):
   a. Natural
   b. None
3. Character of soil surface:
   a. Undisturbed duff
   b. Burned duff
   c. Scarified surface artificially shaded
   d. Mineral soil
4. Seed-destroying rodents and birds:
   a. Completely excluded
   b. No protection

The treatments were assigned to the various subdivisions by accepted methods of randomization. The lay-out of artificially seeded plots on the 2 blocks, representing in replicate 2 degrees of density of tree cover, 2 degrees of density of low cover, 4 kinds of soil surface, 2 years of sowing, 2 tree species, and 2 degrees of protection from rodents and birds, included altogether 256 units upon which germination and survival could be observed, and an equal number of paired plots to be used in growth determination. To check on natural

seeding, a third series of paired plots was established on each block (fig. 1) and left unsown.

Seeding was carried out in 1937 and 1938. The soil surfaces for the 1937 sowings were prepared during May 1937, and those for the 1938 sowings during September 1937. Burning was accomplished by applying a gasoline brush-burning torch to the natural accumulation of wood and litter upon the ground. This left a layer of humus ½ inch to 1 inch deep, a sprinkling of charcoal, and a very thin deposit

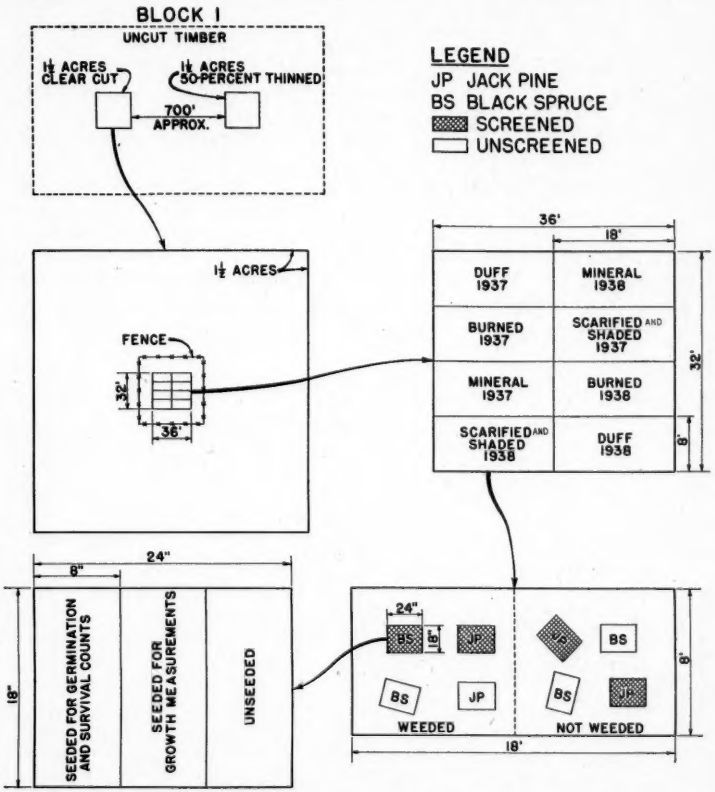

FIGURE 1.—Arrangement of plots in one replication.

of ash, thus closely approximating conditions after a forest fire. Soil acidity tests about 3 weeks later indicated that the pH of the surface material had not been perceptibly affected. Mineral soil surfaces were made ready by stripping away the litter, duff, and humus. Scarified surfaces were prepared by breaking up and mixing the duff, the humus, and a little of the mineral soil. Two layers of sticks were placed crisscross over the scarified surfaces to simulate the shading effect of a light layer of logging slash, concealing approximately 75 percent of the ground surface. The undisturbed duff surfaces re-

quired no preparation. Duff and humus together averaged about 1½ inches thick, varying from less than 1 inch to 4 or 5 inches. The duff was composed of matted conifer needles, leaves, twigs, and mosses in various stages of decay. The whole organic layer was closely interlaced with the roots of trees, shrubs, and herbs.

It was intended that enough seeds be sown to produce about 50 seedlings on each 1-square-foot subdivision. To compensate expected differences in germination, the number of seeds sown per subdivision was varied as follows: Jack pine on mineral, burned, and scarified surfaces, 62; jack pine on duff, 124; black spruce on mineral, burned, and scarified surfaces, 100; black spruce on duff, 200. The seed used in 1938 was from the same lots as that used in 1937. In 1937 the viability of the jack pine seed was 80 percent and that of the black spruce seed was 64 percent; in 1938 the viability of the jack pine seed was still 80 percent, but that of the black spruce seed had dropped to 61 percent.

The 1937 plots were seeded on June 3, 4, and 5, and the 1938 plots in the period May 6–9. The method used was to scratch the surface of the plot lightly with a small stick, scatter the seeds, and pat the surface lightly with the hand to force the seeds into crevices of the loosened surface. This left most of the seeds partly visible except on the duff and the scarified soil, where practically all of them disappeared into crevices. This method may have brought the seeds into slightly closer contact with the soil than natural seeding would have done, but was necessary to prevent excessive washing away of seeds during heavy spring rains.

Screen boxes to give protection from rodents and birds were put in place on half the plots immediately after sowing and left until the end of the first growing season. The type of screen used reduced light intensity by only 10 percent as determined with Shirley's light meter.

Records were taken on block I of maximum and minimum air temperatures, soil surface temperatures, precipitation, evaporation, light intensity, and soil moisture content at various depths. On block II, such measurements were limited to precipitation and soil moisture. Precipitation was measured with rain gages similar to the standard instrument, two being used on the cleared areas and three on the plots having tree cover. Daily maximum temperatures on the four kinds of soil surface were measured on both kinds of cutting, with eight small maximum thermometers, and a continuous record of temperature on the mineral surfaces was kept with two thermographs. Soil moisture was determined partly by the oven-drying method and partly with porous pot tensiometers. Evaporation and light intensity were measured with paired black and white Livingston atmometer spheres, six to eight pairs being used at a time.

Germination and survival counts were started soon after germination began. While the seedlings were small and tender they were counted every 2 or 3 days, but as they increased in size the interval was gradually extended to about 30 days in the third growing season. The small amount of germination that occurred in the second growing season was excluded from the analysis on the assumption that seedlings getting such a late start were of little practical significance. Growth was recorded in terms of height of tops at end of each growing season and, beginning with the second year, in terms of green weight

of tops at end of growing season. To ascertain depth of root penetration, seedlings were dug up at intervals of 7 to 10 days during the growing season of 1937.

GERMINATION

Germination was prompt. In the 1937 series, it began on June 10, 7 days after the seed was sown, and was largely completed by June

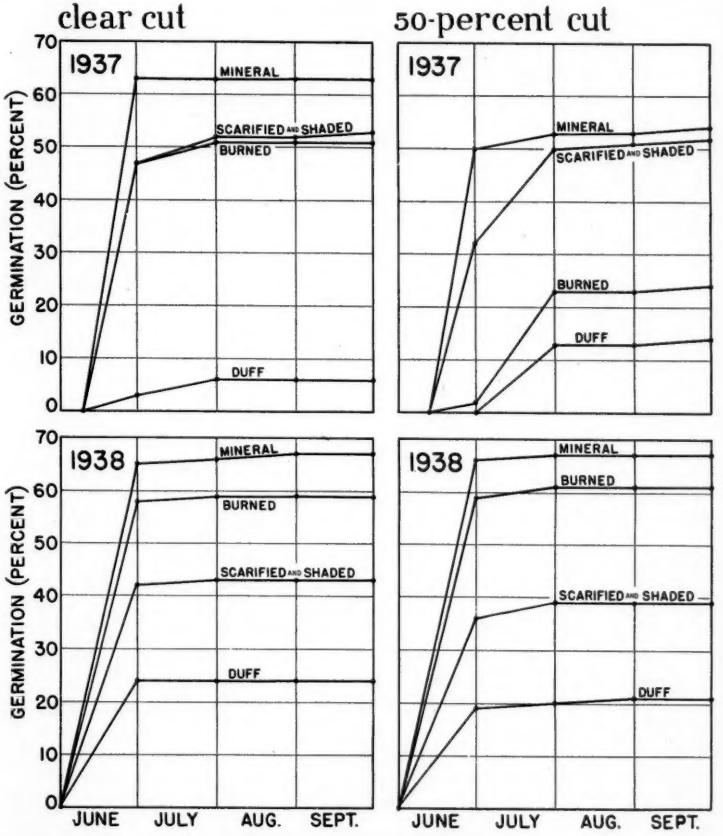

FIGURE 2.—Course of germination of jack pine under various conditions as to soil surface and tree cover in 1937 and 1938.

30. There was, however, some activity during July, and scattered seedlings appeared during August and September (figs. 2 and 3). Jack pine germinated somewhat more promptly than black spruce. In the 1938 series, germination began on May 30, 24 days after sowing, and was practically completed by the end of June.

The somewhat earlier and more complete germination in 1938 was apparently the result not only of earlier sowing but also of more

abundant precipitation during June of that year (table 1). The longest period in June without at least a trace of precipitation was 3 days, consequently germination progressed rapidly. The heavy precipitation in July 1937 (table 1) gave seeds a further opportunity to germinate, but in July 1938 rainfall was only about half of normal and germination stopped abruptly. Both species germinated promptly whenever temperature and moisture conditions were favorable. This

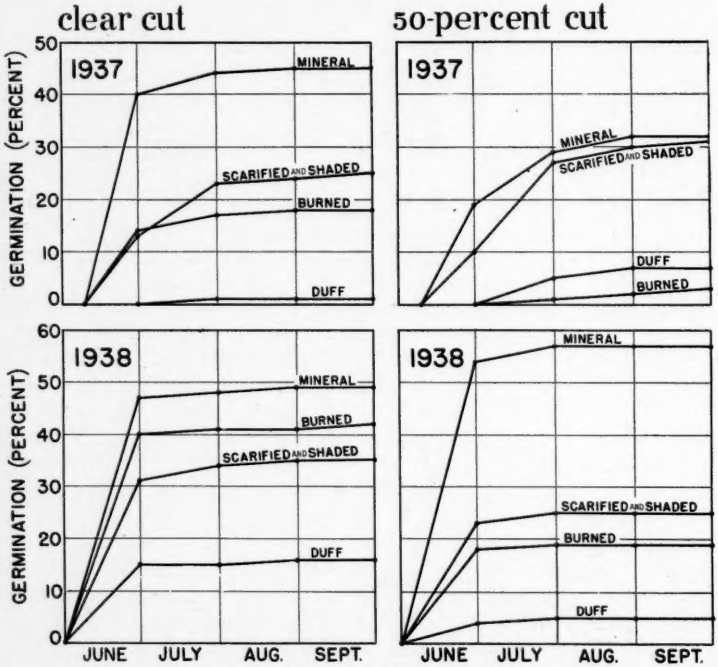

FIGURE 3.—Course of germination of black spruce under various conditions as to soil surface and tree cover in 1937 and 1938.

observation may be of considerable practical importance in planning natural-regeneration operations, especially because of the peculiar seeding habits of both jack pine and black spruce. In the case of jack pine, release of seed by the serotinous cones can be brought about by lopping and scattering the slash after logging (*11*). The peculiarity of black spruce seed dissemination is that after the seed has ripened it is dispersed slowly and continuously over a period of 2 or 3 years (*9*). It is likely, therefore, that some recently escaped black spruce seed will always be present when the timber is cut, regardless of time of year.

TABLE 1.—*Monthly precipitation on study area during growing seasons* [1]

Month	1937	1938	1939
	Inches	*Inches*	*Inches*
May	3.72	3.51	4.70
June	1.11	3.66	4.44
July	5.03	2.00	2.24
August	4.69	3.12	6.76
September	3.68	1.71	3.85

[1] Rain gage was located on clear cutting, block I

Although germination was prompt, it was only moderately complete (table 2). The overall germination of jack pine (44 percent) was considerably better than that of black spruce (26 percent); this is largely accounted for by the difference between the initial viability percentages of the two species, 80 and 62.5.

TABLE 2.—*Average germination in relation to soil surface, 1937 and 1938*

Soil surface	Jack pine	Black spruce	Average
	Percent	*Percent*	*Percent*
Mineral	63	46	54
Burned	49	20	35
Scarified and shaded	47	29	38
Duff	17	7	12
Average	44	26	35

So little germination of naturally disseminated seeds took place on the unsown plots as to make it appear certain that natural seeding had not materially increased stocking on the artificially seeded plots.

Germination varied strikingly with soil surface, but both jack pine and black spruce reacted quite consistently to the different soil conditions, as shown by the averages of both years in table 2. Mineral soil proved to be decidedly the most favorable medium and duff the poorest for both species, for both years of sowing, and on both clear-cut and 50-percent-cut areas (figs. 2 and 3). The comparative responses on burned duff and scarified-shaded duff were less consistent. In 1937, when precipitation during June was deficient, scarified-shaded duff made the better showing, but in 1938, when June rainfall was heavy, better germination occurred on the burned duff. Because the layers of crossed sticks retarded evaporation, by reducing air movement and lowering temperature, scarified-shaded duff was almost as favorable a medium as mineral soil in 1937, but had a superabundance of moisture in 1938.

The growing seasons of 1937 and 1938 by no means represent the extremes of dryness and wetness for northeastern Minnesota, but the differences were sufficient to give an idea of the influence of rainfall distribution during the germination period.

The germination responses to the different media correspond to the moisture-holding characteristics and textures of the media. Mineral soil offered the least resistance to the transfer of water to the seeds and undisturbed duff the most. The wilting coefficients

(as determined by the standard centrifuging method) of the mineral soil, scarified duff, burned duff, and undisturbed duff were 14, 54, 56, and 77 percent, respectively. Furthermore, mineral soil has the finest texture, which permits closer contact with the seeds and thus facilitates the transfer of moisture. The ashes and bits of charcoal in burned duff and the admixture of mineral soil in scarified duff made these materials intermediate to mineral soil and undisturbed duff in respect to wilting coefficient and texture.

Protective screening against seed-eating birds and rodents had a rather surprisingly small effect on germination. On screened and unscreened plots, respectively, germination percent averaged 48 and 40 for jack pine, 27 and 24 for black spruce. The effort to find out the effect of seed destruction by birds and rodents resulted less conclusively than any other phase of the experiment, probably because the interval between sowing and germination did not give seed eaters the normal opportunity to locate the seed. Also, the population and food habits of birds and rodents may vary considerably from year to year, and during the time of the experiment these variations may have been in a favorable phase.

The influence of tree cover and that of low cover on germination were not of practical consequence. They were nearly the same for both species.

Altogether, the results of germination counts indicate that (1) shade, as from crossed sticks (logging slash), is beneficial to germination in dry seasons; (2) germination on duff, both natural and burned, is better in wet seasons than in dry seasons; (3) mineral soil is the most consistently reliable medium for germination among the four studied; and (4) undisturbed duff is the poorest.

SURVIVAL

Seedlings began to die within a few days after the first ones appeared. Survival averaged 75 percent at the end of June, 56 percent at the end of July, and 42 percent at the end of August; but from August 31 of the first growing season to September 30 of the second only 4 percent of the original number of seedlings died, leaving a net survival of 38 percent. Although total mortality varied considerably between species, and greatly between the two degrees of tree cover and among the four kinds of soil surface, the time of year when mortality occurred was practically uniform (figs. 4 and 5). The loss during the third growing season (data from 1937 series only) was less than 1 percent. It is evident that the first 3 months after germination are the most critical period in seedling establishment.

As would be expected, jack pine materially exceeded the smaller black spruce in capacity to survive, survivals at the end of the second growing season for the pine and the spruce being 54 percent and 22 percent, respectively. This suggests that regeneration of black spruce requires either greater amounts of seed or more favorable environmental conditions then equally successful regeneration of jack pine. In general, survival of both species followed the same trends in relation to the various environmental conditions; a condition harmful to one species was usually harmful to the other.

Over-all survival of both species during the first 2 years varied most strikingly with soil surface (figs. 4 and 5), averaging 65 per-

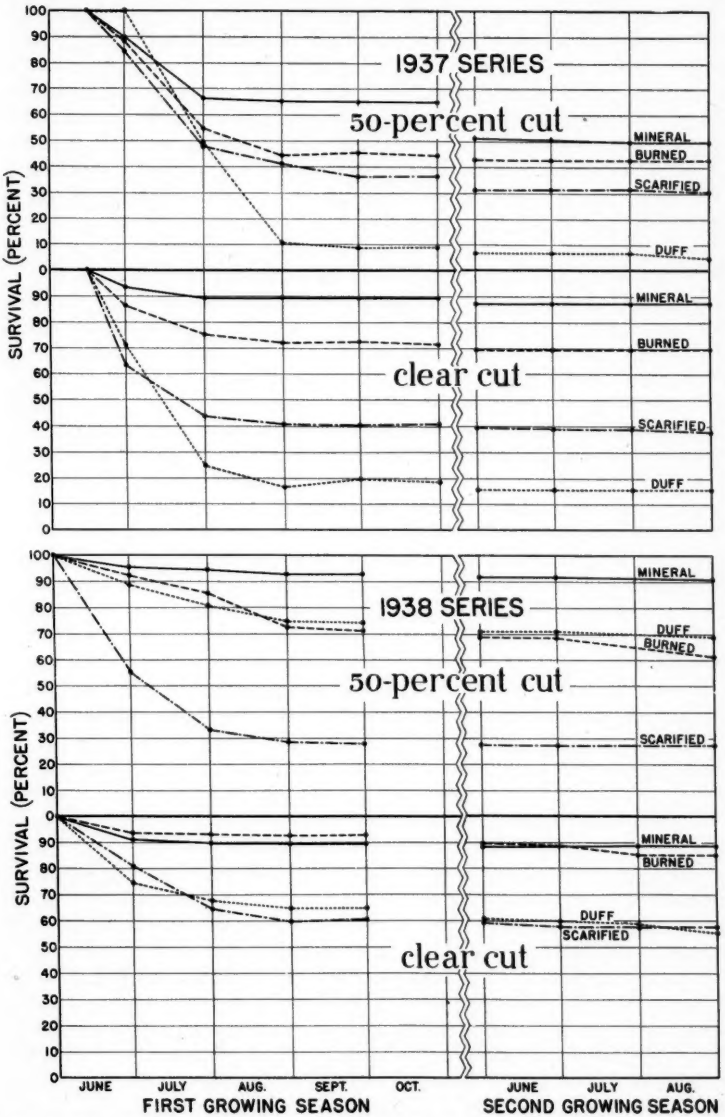

FIGURE 4.—Survival during first and second growing seasons of jack pine seedlings on various soil surfaces and on areas clear cut and 50-percent cut.

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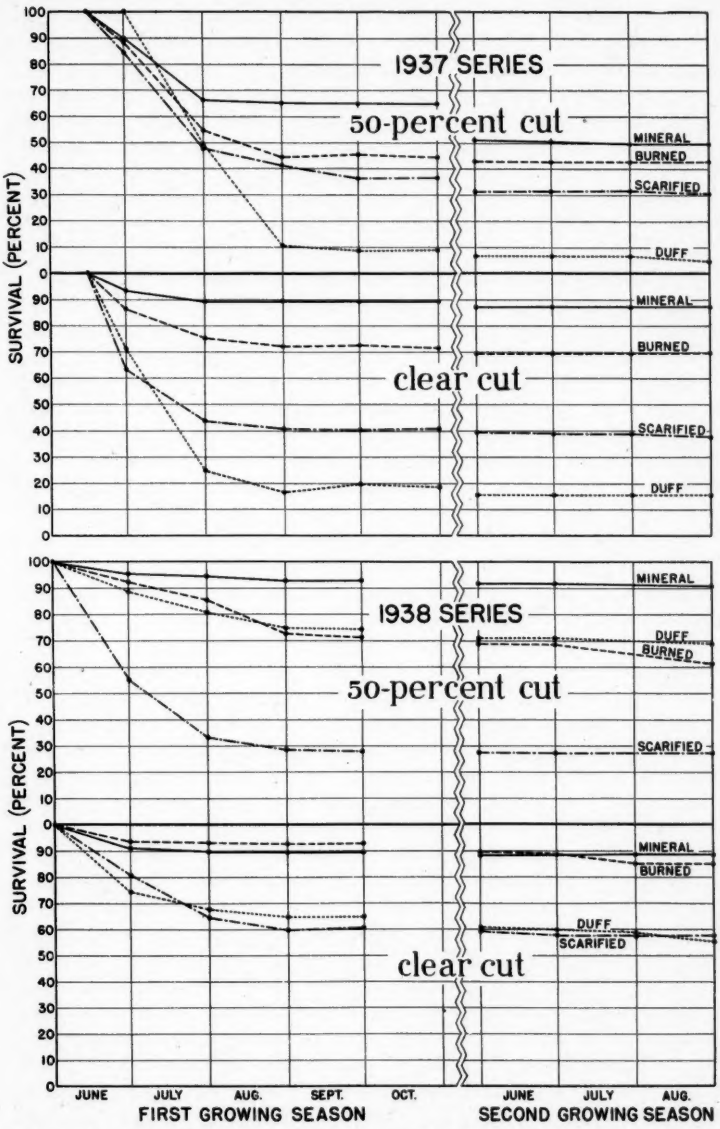

FIGURE 4.—Survival during first and second growing seasons of jack pine seedlings on various soil surfaces and on areas clear cut and 50-percent cut.

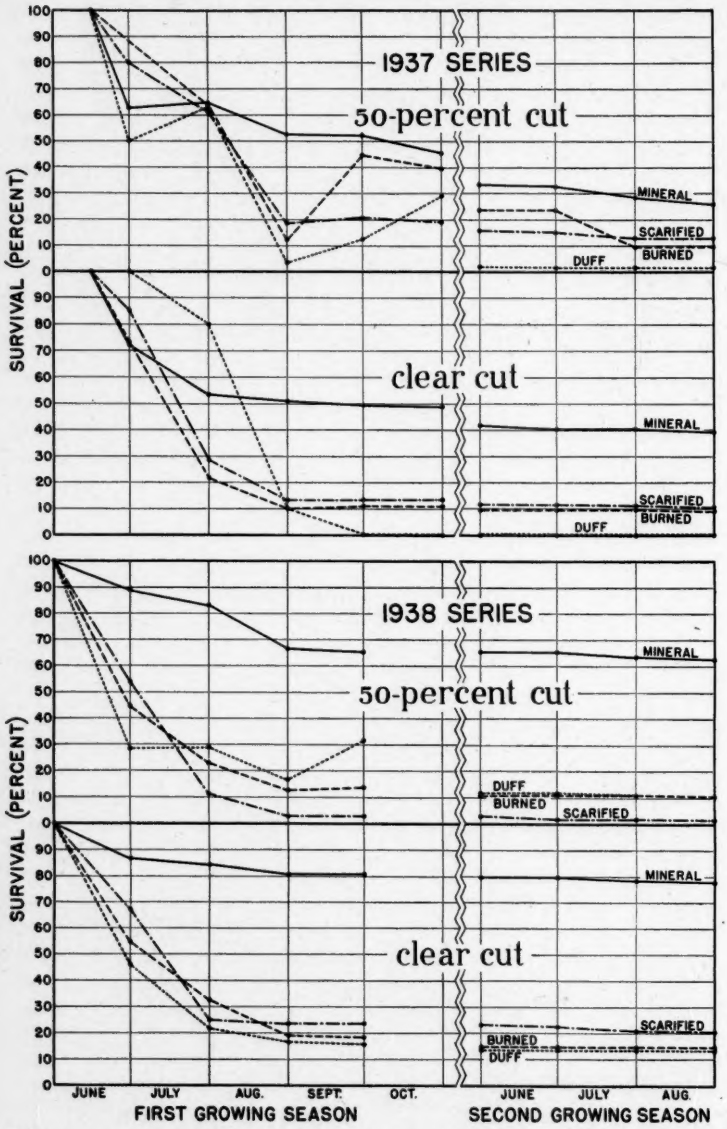

FIGURE 5.—Survival during first and second growing seasons of black spruce seedlings on various soil surfaces and on areas clear cut and 50-percent cut.

cent on mineral soil, 37 percent on burned duff, 25 percent on scarified and shaded soil, and 24 percent on undisturbed duff. The advantage of mineral soil with regard to survival, as well as to germination, makes this kind of surface outstandingly superior for seedling establishment. The chance that a seed will germinate and the seedling survive 2 years is 12 times as great on mineral soil as on undisturbed duff. It may be noted that methods for exposing the mineral soil with power machinery as a practical silvicultural measure are already well developed (*2*).

Tree cover had considerable influence, the percentages for clear-cut and partially cut plots being 45 and 32, respectively. There was a great difference in 2-year survival between the two annual sowings, the average for the 1937 series being 30 percent and that for the 1938 series 46. The better showing of the 1938 series apparently resulted from the earlier germination (figs. 2 and 3) and the heavier rainfall during June (table 1).

CAUSES OF MORTALITY

The relations of soil surface, tree cover, and low cover to seedling survival assume a more significant aspect when the specific causes of mortality are considered, because damage by each of the chief destructive agents, both biotic (insects and damping-off fungi) and physical (heat and drought), was apparently affected by one or more of the controlled conditions. The recorded causes of death and frequency of each are as follows:

	Percent		*Percent*
Insects	52	Mildew	2
Damping-off fungi	17	Root rot	1
Heat	10	Plant competition	(trace)
Drought	8	Miscellaneous	3
Frost heave	3	Unknown	4

A good many seedlings were killed by combinations of factors, and sometimes no cause could be identified with certainty. However, these uncertainties were relatively infrequent and do not affect the principal conclusions. To a considerable extent the main causes of mortality—insects, damping-off fungi, heat, and drought—operated concurrently, and hence "competed" among themselves. Particularly if there had not been such exceedingly high insect losses, the other agents probably would have disposed of more seedlings.

The distribution of losses due to each cause with regard to species, tree cover, and soil surface, in percent of total germination, is shown in table 3.

TABLE 3.—*Mortality* [1] *(percent) during first 2 years, by species and cause, in relation to tree cover and soil surface*

Species, tree cover, and soil surface	Insects	Damping-off	Heat	Drought	Frost heave	Mildew	Root rot	Competition	Miscellaneous	Unknown	Total
Jack pine:											
Clear cut:											
Mineral	5.9	2.0	0	0.5	0.4	0	0.4	0.1	1.8	0.4	11.5
Burned	8.7	6.3	.6	1.3	.2	2.2	.1	2.0	0	1.2	22.6
Scarified	39.7	5.4	.2	1.5	0	1.2	.6	.2	.2	3.4	52.4
Duff	37.7	5.2	3.0	3.7	0	1.6	.6	2.0	3.2	7.2	64.2
Average	23.0	4.7	1.0	1.8	.2	1.2	.4	1.1	1.3	3.0	37.7
50-percent cut:											
Mineral	7.8	4.2	.1	8.4	7.3	0	.3	0	.6	1.3	30.0
Burned	17.2	14.7	5.0	7.1	0	1.2	2.0	.6	4.4	1.0	53.2
Scarified	50.0	12.4	.6	4.1	.1	1.1	.6	0	2.3	1.4	72.6
Duff	38.1	14.6	3.0	4.4	0	2.3	0	0	1.1	.4	63.9
Average	28.3	11.5	2.2	6.0	1.8	1.1	.7	.2	2.1	1.0	54.9
Average jack pine	25.6	8.1	1.6	3.9	1.0	1.2	.6	.6	1.7	2.0	46.3
Black spruce:											
Clear cut:											
Mineral	17.3	8.7	1.9	3.1	4.0	.2	.8	0	2.2	3.1	41.3
Burned	36.1	17.7	24.6	4.3	0	.8	1.7	.4	2.3	2.1	90.0
Scarified	67.1	11.0	.6	1.0	0	.8	.8	0	1.2	1.6	84.1
Duff	44.6	9.8	22.6	5.0	0	.1	.4	0	.6	0	83.1
Average	41.3	11.8	12.4	3.3	1.0	.5	.9	.1	1.6	1.7	74.6
50-percent cut:											
Mineral	19.7	3.1	.4	17.6	9.3	0	1.2	0	2.4	2.4	56.1
Burned	25.2	13.9	27.4	3.9	0	10.4	.1	0	6.2	2.8	89.9
Scarified	61.5	22.7	.3	5.0	.3	.8	.4	.1	.6	1.2	92.9
Duff	54.9	14.7	5.4	3.8	3.1	.8	.4	0	.4	8.5	92.0
Average	40.3	13.6	8.4	7.6	3.2	3.0	.5	0	2.4	3.7	82.7
Average black spruce	40.8	12.7	10.4	5.5	2.1	1.7	.7	.1	2.0	2.7	78.7
Average both species	33.2	10.4	6.0	4.7	1.5	1.5	.6	.3	1.8	2.4	62.4

[1] In terms of total germination.

INSECTS

Insects, causing half the mortality, were by far the most important source of seedling losses. Insects actually observed eating the tops of young seedlings were a species of grasshopper (*Camnula pellucida*), some very small caterpillars (*Halisidota* spp.), the larvae of a sawfly (*Empria* spp.),[7] and the spruce budworm (*Cacoecia fumiferana*). One small larva, not identified, ate 17 spruce seedlings on 1 plot within 11 days. A few seedlings were killed by larvae of June beetles (*Phyllophaga* spp.).

Loss of tops and cotyledons through insect activity began immediately after the first seedlings appeared, and continued through July and August. At first it was thought that birds might be causing some of the loss, but frequent observations and the similarity of damage on screened and unscreened plots led to the conclusion that insect activity was the sole cause. The total damage attributed to insects was practically equal on screened and unscreened plots.

[7] The three insects just named were identified by A. G. Ruggles, State entomologist, Minnesota Department of Agriculture, Dairy, and Food.

Insects are recorded to have killed approximately 26 percent of all the jack pine that germinated and 41 percent of the black spruce, but since some seedlings may have been killed by other agents before the insects had a chance at them, the reported values (table 3) may not show the full possible effect of insect damage.

Insect-caused mortality was affected very little by tree cover, and was not appreciably greater on unweeded than on weeded plots; but it varied to a surprising extent with soil surface. Losses were greatest on the scarified-shaded surfaces, next greatest on undisturbed duff, less on the burn, and least on mineral soil. These differences were large and fairly consistent for both species, both degrees of tree cover, and both degrees of low cover.

Why should the nature of the soil surface affect insect damage? There appear to be several possible explanations. With the exception of grasshoppers, all the insects observed feeding were small larvae having little ability to travel. Probably these insects had wintered (either as eggs or as larvae) very close to where they attacked the seedlings. Overwintering larvae or eggs would of course be destroyed by burning the duff or removed in the process of preparing the mineral soil surface. This could easily account for the light damage on the burned duff and mineral soil and offers an additional explanation for the fact that reproduction is frequently successful after forest fires. If insects migrated to the plots after the surfaces were prepared, they may have preferred the irregularity and loose structure of the scarified soil and the undisturbed duff. Neither of the explanations suggested would account for the greater losses on scarified-shaded soil as compared with undisturbed duff. Possibly the sticks laid over the scarified surfaces provided some element of comfort or protection that encouraged the insects to concentrate or permitted them greater activity.

The fact that insects killed about 60 percent more black spruce than jack pine may indicate a species preference. More probably it was due to the smaller size of the spruce seedlings, because of which they were easier to kill and a larger number were required to provide an equal quantity of food.

The most likely reason why low vegetation had little or no effect on seedling damage by insects is the fact that during the early part of the first growing season the low vegetation was rather sparse, owing to the recent soil surface preparations, and could hardly exert a strong influence until much of the insect damage had been done.

Damping-Off Fungi

Damping-off fungi, the second most important cause of mortality, killed somewhat more black spruce than jack pine. Losses were generally lowest on mineral soil. They were greater under tree cover than in the clearings, particularly among jack pine seedlings, but the data are too erratic to justify drawing conclusions.

Heat

Although heat caused only 10 percent of the total mortality, it gave evidence of being potentially a very serious source of seedling injury. Losses on mineral soil and on scarified soil were consistently so small

as to be negligible, but those on undisturbed duff and on burned duff, particularly the latter, were considerably higher. Temperature measurements explain this. Daily maximum temperatures on the undisturbed duff and burned duff surfaces frequently exceeded 120° F. and occasionally exceeded 140°. The highest temperatures observed on undisturbed duff and burned duff during both seasons were, respectively, 153° and 159°. On the other hand, the temperatures of mineral soil and scarified-shaded soil seldom went above 100°.

The greatest number of low daily maximum temperatures occurred on the scarified-shaded soil, obviously as a result of the heavy shade cast by the two layers of sticks. The relatively low temperatures on the mineral soil are largely accounted for by the cooling effect of evaporation. Conversely, the relatively high temperatures on the undisturbed duff may have been due to the dryness of this material, which permitted little such cooling. The dark color of the burned duff may explain in part the relatively high temperatures on that surface. Contrasts in color of the various materials, however, were not nearly so striking as that described in a report by Isaac (*6*) on a seedling-establishment study. Here the mineral soil was a yellowish brown, the undisturbed duff was a light grayish brown, and the burned duff was a mixture of black and grayish brown. The differences in color were apparently not great enough to cause very much variation in temperature.

As would be expected, the tiny black spruce seedlings proved decidedly more sensitive to heat than the relatively large jack pines.

Observed losses due to heat were too few in number to justify definite conclusions. Heat losses were practically the same under the 50-percent tree cover as on the cleared areas. This is not surprising, for measurements showed that daily maximum surface temperatures were almost as high under tree cover as in the clearings. Tree shadows passing over the bulb of the soil thermograph caused very rapid fluctuations in the temperature record, but during shadow-free periods the temperatures recorded on the timbered and clear-cut areas were practically the same. Although the succession of shadows considerably shortened each daily exposure to lethal temperatures, this did not affect survival. In seasons having longer periods of hot weather the results would probably be different. Failure of the partial tree cover to restrict maximum surface temperatures greatly can be accounted for only by the somewhat drier condition of the surface soil under the trees.

Drought

Drought, like heat, was decidedly not a limiting factor in seedling establishment in this study. It caused only 8 percent of the total deaths. The fact that the July 1938 rainfall of only 2 inches (approximately half of normal) was sufficient for most of the seedlings suggests that drought is not a common limiting factor in northeastern Minnesota. Although the losses were too light to provide decisive evidence, they are suggestive of the effect of drought in critically dry years. Most drought losses occurred soon after germination. Mortality due to drought was higher in spruce than in pine, and higher under tree cover than on the clear-cut areas (table 3). It did not vary consistently with soil surface. It was higher on unweeded plots than on weeded plots.

The indication that soil surface material does not greatly influence drought losses is corroborated by data taken by Barr (*1*) showing that spruce seedlings endured an artificially maintained drought as long in humus soil from a spruce forest as in clay soil and sand soil.

Soil moisture determinations made by the oven-drying method during the 1937 growing season indicated that moisture was generally present in quantities adequate for survival. The moisture content tended to be a little higher on the clear-cut areas than on the areas having tree cover, although the differences were so small as to appear inconsequential.

The study of drought mortality, which included the digging of seedlings at frequent intervals to determine extent of root penetration, failed to bring out any consistent relation between progress of the season and drought resistance of the seedlings. Several reasons for this may be cited: (1) the frequent summer rains typical of northeastern Minnesota prevented establishment of anything like a regular moisture gradient in the soil. (2) The several horizons (including duff and humus) in the upper 3 inches of soil varied so greatly in texture, wilting coefficient, and thickness that it was most difficult to determine whether moisture was available during critical periods. (3) Even within relatively small samples (50 to 75 gm. dry weight) of organic soils that show little or no available moisture, there are likely to be fractions, such as small dead roots and decayed wood, from which seedlings can extract water. Seedling rootlets showed a decided tendency to follow the inside surfaces of dead roots and to grow into rotten wood. (4) Because scattered seedlings continued to appear throughout the summer and, in 1937, through early autumn, the seedlings were never at a uniform stage of development, and so presumably were never uniform in drought resistance.

The black spruce seedlings extended their primary rootlets downward about 0.5 inch, and thus gained some protection against superficial drying of the soil, within a week after germination. Additional downward growth, however, was slow, and at the end of the first growing season few seedlings had penetrated to a depth greater than 2.5 inches. Most of the roots developed in horizontal planes, and only a few entered mineral soil except on the plots where the mineral soil was exposed. The primary roots of jack pine penetrated more rapidly and to a considerably greater depth than those of black spruce. During the first 10 days they extended downward from 1.4 to 1.8 inches, and by the end of the first growing season they had reached depths of 4 to 7 inches. Although a considerably greater proportion of the jack pine than of the black spruce roots grew down into the mineral soil, the jack pine formed an extensive system of lateral roots in the humus soil on the burned, scarified, and undisturbed duff surfaces.

From the observations made on root development, it is evident that an extended drought causing the soil to dry out to a depth of 3 inches would probably result in an almost complete loss of 1- and 2-year black spruce seedlings. Jack pine is probably less subject to killing by drought than black spruce, because of its deeper-root penetration.

Frost Heave

Frost-heave losses occurred almost exclusively on mineral soil, and more commonly under tree cover than on the clear-cut plots (table 3).

The losses were greater in ratio to the total number of seedlings exposed than the tabulated data indicate, because many seedlings died from other causes before frost heave occurred. This is especially true of black spruce under tree cover. The longer roots of jack pine account for its lighter mortality. Frost heave disturbed trees much more commonly than it actually killed them. Many seedlings lifted almost free of the soil nevertheless managed to survive.

Other Causes

Early spring examination at the beginning of the second growing season disclosed that a small number of seedlings of both species had been killed apparently by fungus organisms, which had formed mats of mycelia over the needles and buds. The roots of these seedlings were quite sound and strong, indicating that they had not died until after the tops were killed. These losses, attributed in table 3 to mildew, were confined almost entirely to the three organic surfaces. For the most part the affected seedlings, were the smaller and weaker ones on the unweeded plots. Losses attributed to root rot were caused by some unidentified factor that killed the seedling roots of both species on all four kinds of soil surface, but chiefly among the smallest and weakest seedlings on the unweeded plots.

The few seedlings classified as killed by plant competition were small, suppressed, and severely crowded.

"Miscellaneous" causes, to which a very small part of the mortality was attributed, included flooding, washing, failure of radicle to enter the soil after the seed germinated on the surface, abnormal germination, mechanical injury by falling sticks, trampling by deer, and smothering by leaves. The fences around the plots afforded almost complete protection against deer, snowshoe hares, and woodchucks.

TOP GROWTH

The most contrasting results in this experiment occurred in the phase concerned with top growth (fig. 6). The growth of seedlings was observed under almost optimum conditions, and under conditions in which life could barely be sustained. The most notable feature of the growth phase was the excellent response of both species to complete removal of tree cover and low cover.

HEIGHT OF 1-YEAR-OLD SEEDLINGS

The average height of 1-year-old jack pine seedlings on the clear-cut plots was 2.4 inches, as compared with 1.4 inches on the partial cuttings. On the weeded plots seedlings averaged in the first year 2.1 inches, and on the unweeded plots 1.7 inches. On clear-cut weeded plots the average was 2.7 inches, as compared with 1.3 inches on partially cut, unweeded plots. The better growth on clear-cut weeded plots was probably due to more favorable moisture, light, and temperature conditions in the open. Under heavy herbaceous vegetation, light intensities were undoubtedly much lower than the 43 percent recorded under the 50-percent tree cover.

Jack pine seedlings on the scarified-shaded plots averaged 1.5 inches in contrast to approximately 2 inches for those on the burned duff, natural duff, and mineral soil. The difference was clearly due to the unfavorable shading effect of the crisscrossed sticks. Once the seedlings had developed to a fair height above the sticks, they grew as

rapidly as any others. The small size of these seedlings probably made them more susceptible to various agents of injury. The 1938 series averaged 40 percent greater in height at the end of the first growing season than the 1937 series, owing, no doubt, to the earlier date of sowing in 1938, which lengthened the growing season by 2 to 3 weeks.

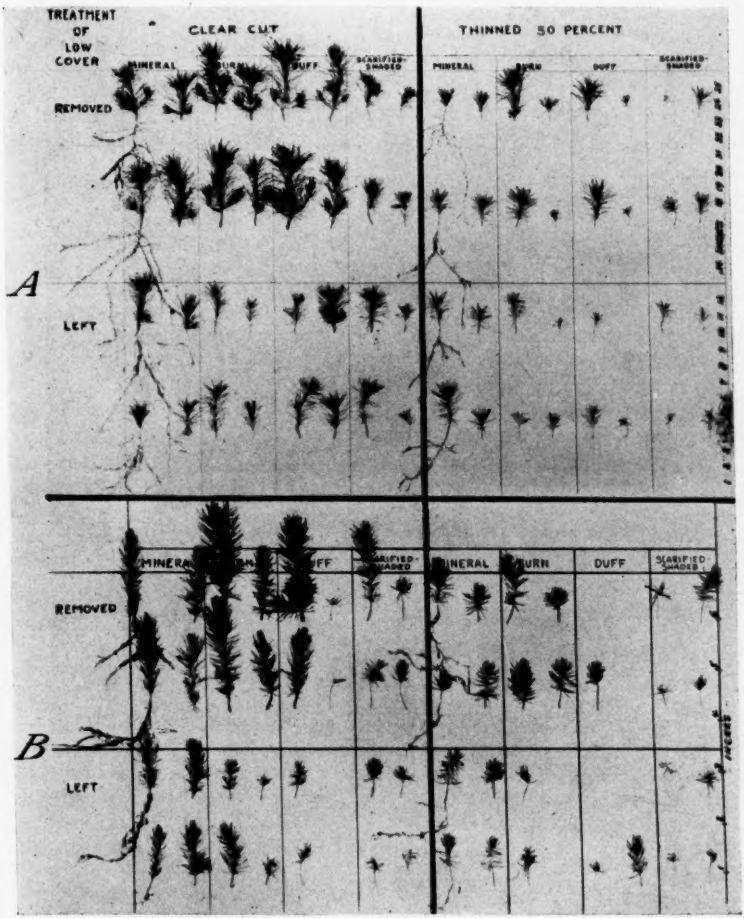

FIGURE 6.—Representative seedlings (*A*) of jack pine and (*B*) black spruce, illustrating comparative development during first growing season (1938) under various conditions as to tree cover, low cover, and soil surface. The two species are shown on different scales, to permit inclusion in the same figure.

Spruce followed growth trends similar to those of jack pine, although its growth was not nearly so great. For instance, heights of 1-year-old seedlings averaged 1.0 inch on clear-cut plots and 0.6 inch in the partial cuttings. It would appear safe to infer that the same factors affected growth of both species in about the same degree.

WEIGHT AND HEIGHT AT 2 YEARS

By the end of the second season, the jack pine seedlings growing under the more favorable conditions had far outstripped the others in

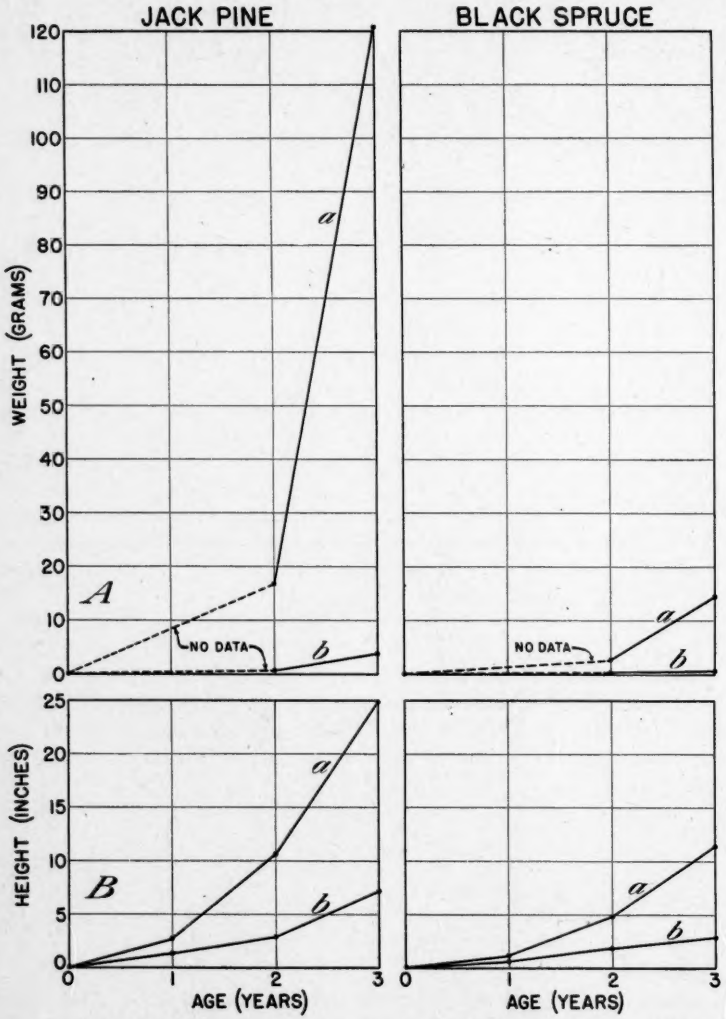

FIGURE 7.—(*A*) Average green weight of tops and (*B*) average height of tops of jack pine and black spruce on (*a*) clear-cut weeded plots and (*b*) 50-percent-cut unweeded plots.

weight and height (fig. 7, table 4). Clear cutting and weeding both proved beneficial independently, and the two treatments combined gave outstandingly good results. Weeding resulted in a great advan-

tage in weight on all four kinds of soil surface, but especially on the burned and the undisturbed duff. Weight of tops at the end of the second growing season did not vary appreciably with year of sowing.

TABLE 4.—*Average green weight of tops of 2-year-old seedlings in relation to low cover, tree cover, and soil surface*

Tree cover and surface condition	Jack pine			Black spruce		
	Weeded	Not weeded	Average	Weeded	Not weeded	Average
Tree cover:	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
Clear cut	16.82	2.60	9.71	2.49	0.22	1.36
50-percent cut	3.51	.55	2.03	.23	.14	.18
Average	10.16	1.58	5.87	1.36	.18	.77
Soil surface:						
Mineral	8.28	2.52	5.40	.96	.24	.60
Burned	13.72	1.19	7.46	1.81	.16	.98
Scarified and shaded	8.23	1.09	4.66	.52	.12	.32
Duff	13.15	1.46	7.30	4.15	.10	2.12
Average	10.84	1.56	6.20	1.86	.15	1.00

The green weight of the tops of 2-year-old seedlings was much less for black spruce than for jack pine, but the relative responses to tree cover, low cover, and soil surface were very similar (table 4, fig. 7). For black spruce, as for jack pine, the combined effect of absence of tree cover and absence of low cover was much greater than the effect of either of these conditions alone.

Both jack pine and black spruce seedlings growing on mineral soil were appreciably less tall at 2 years than those growing on undisturbed duff and burned duff. It is believed that this was due to a deficiency in some nutrient, probably nitrogen, caused by the removal of the humus, since the seedlings on the organic surfaces had a darker green color from the time they were a few weeks old.

HEIGHT AND WEIGHT AT 3 YEARS

At 3 years, jack pine excelled black spruce in height and weight of tops by a greatly increased margin (fig. 7). The tops of jack pine seedlings on the clear-cut and weeded plots averaged 25 inches in height and 121 gm. in weight; the corresponding values for black spruce tops were 12 inches and 14 gm. The tallest individual 3-year-old jack pine seedling observed was 32 inches high, and the heaviest one weighed 343 gm. These were free-grown seedlings from clear-cut, weeded plots having undistrubed duff surfaces. The largest single 3-year-old black spruce seedling was 18 inches tall and weighed 77 gm. It grew on a clear-cut, weeded plot having a burned surface.

On unweeded plots in the 50-percent cuttings, the weights of 3-year-old jack pine and black spruce seedlings averaged only 3.8 gm. and 0.2 gm., respectively. Obviously, such meager seedlings are unthrifty and have little chance of success.

CONCLUSIONS

The results of the experiment reported herein indicate that:

(1) Seedlings of jack pine and black spruce respond much the same to the chief environmental factors, although the jack pine seedlings,

being larger and faster growing, have a somewhat better chance of survival and establishment. In fact, the similiarity of the responses of the two species, in germination, survival, and growth, confirms the finding in an earlier study (*9*) that black spruce is capable of functioning as a fire species in northern Minnesota in much the same manner as jack pine.

(2) For these species bare mineral soil is the best of the four germination media tested, burned duff and scarified-shaded duff are somewhat less reliable, and the natural forest floor is the poorest. Seedlings do not grow so rapidly on mineral soil as on the three other kinds of surface material.

(3) Absence of both tree cover and lower plant cover favors establishment and growth during summers in which rainfall is not seriously deficient.

(4) Insects are the chief cause of early mortality. Damage by insects is particularly serious on scarified-shaded duff and undisturbed duff.

In practical terms, it appears that the best conditions for establishment and growth of reproduction of these species will be created by tearing up the ground surface to expose mineral soil and clear-cutting the timber. In order that tree reproduction may be subjected to the least competition from vegetation that invades clear-cut areas, its establishment should be brought about promptly.

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THE EFFECT OF WATER DEFICITS IN THE TREE UPON MATURITY, COMPOSITION, AND STORAGE QUALITY OF BOSC PEARS [1]

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INTRODUCTION

Information concerning the effects of water supply during the growing season on the storage and dessert qualities of tree fruits is rather limited. Such reports as are available were reviewed in a previous publication (*1*).[2] In adobe clay Anjou pears were, in general, slightly more astringent, more acid, and more highly flavored when appreciable water deficits occurred near harvest than when water deficits were minimized by more frequent irrigation (*1*). The effects of continued, appreciable water deficits on Bartlett pears in both adobe clay and sandy loam were a slight increase in acidity and flavor and a marked reduction in core break-down (*6*).

Although Bosc pears are grown principally in the Hood River and Rogue River Valleys in Oregon, and to a lesser extent in Eldorado, Santa Clara, and Placer Counties in California, where summer irrigation is necessary, the relation of irrigation to the high quality that Bosc pears can attain has not been determined previously. In 1936 and 1937 the effect of irrigation upon the quality of Bosc, as well as of Anjou (*1*) and Bartlett (*6*), was studied in the Rogue River Valley. The effects of water deficits upon the flavor, firmness, water and sugar content, acidity, and carbon dioxide output of Bosc pears during storage are reported herein.

MATERIAL AND METHODS

ESTABLISHMENT OF PLOTS

Plots of Bosc pears were established in the Kenly orchard, located on the floor of the Rogue River Valley, where the soil is classified as Meyer adobe clay, and in the Topsides orchard, located in the rolling foothills on the west side of the Valley, where the soil is classified as Siskiyou coarse sandy loam. The trees in the Kenly orchard were large and moderately vigorous; those in the Topsides orchard were smaller but moderately vigorous. In each orchard three trees were located on a wet plot and three on a dry plot.

The irrigation needs for the wet plots were determined by measuring 45 tagged fruits (15 per tree) per plot every 3 or 4 days and calculating the rate of enlargement. Water was applied whenever the growth rate of the fruits began to slacken. A midseason irrigation was applied to the dry plot on sandy loam in 1936, but this plot was not irrigated in 1937. The dry plot on adobe clay was not irrigated in either season.

[1] Received for publication December 1, 1942.
[2] Italic numbers in parentheses refer to Literature Cited, p. 133.

SELECTION OF FRUIT SAMPLES

Pickings for the determination of storage and dessert quality and chemical composition were made at definite intervals after full bloom. During 1936 the pickings were made 135, 145, and 155 days after full bloom, and in addition an attempt was made to harvest fruit from each plot when it reached a firmness of 14, 13, and 12 pounds as measured by the United States Department of Agriculture pressure tester with the $\frac{5}{16}$-inch plunger. Picking according to pressure test did not appear to be satisfactory; so during 1937 pickings for the determination of quality were confined to 5- to 10-day intervals 126 to 155 days from full bloom.

At 10-day intervals, beginning 126 days after full bloom, a packed box from each plot was placed in storage at 31° F. for later ripening and examination. During November part of the fruit from each box was removed to a warm room (65° to 70°) for ripening, in order that quality might be determined during the period when prime dessert quality might be expected. Additional samples were ripened at later dates for comparison of the decline in dessert quality and the development of physiological disorders.

To measure fruit firmness, representative samples of 15 fruits from each plot were selected at 3-day intervals during a period beginning considerably in advance of commercial harvest. Two determinations were made on peeled areas on the sides of each fruit by means of the pressure tester previously mentioned.

For the determination of chemical composition samples of 20 representative fruits were selected at 10-day intervals. Sections for dry weight were obtained by means of a 6-mm. cork borer. Transverse sections removed from the equatorial region of each fruit were trimmed of core and epidermal tissue and dried for 72 hours at 70° C. without vacuum. Samples for chemical determination were removed with a 15-mm. cork borer in the same manner. After removal of core and epidermal tissue the plugs were ground in a food chopper and a weighed amount of the tissue was preserved in alcohol for sugar determination. The juice was recovered from the remaining tissue by straining through several layers of cheesecloth; aliquots of this juice were used for the determination of pH and titratable acidity.

ANALYTICAL METHODS

Titratable acidity was determined on a 25-ml. sample of juice by dilution with 75 ml. of distilled water and by titration with N/10 sodium hydroxide; methyl red was used as the indicator.

Reducing sugars were determined by the Quisumbing and Thomas (*5*) reduction procedure and the Shaffer and Hartmann (*8*) titration technique. Sucrose was determined by difference in copper-reducing power before and after acid inversion. Determination of glucose and levulose was accomplished by using the iodine-oxidation method as developed by Lothrop and Holmes (*4*).

Hydrogen-ion concentration was measured by comparison with a standard cell in a pH meter with a saturated quinhydrone electrode. The index figure represents the ratio of the dissociated to the total acid present, which, according to Du Toit and Reyneke (*2*), is of value in the determination of harvest maturity.

Carbon dioxide output of the pears in 31° F. storage was measured by a modified "Truog tower" method as described in a previous publication (*1*). Determinations were made on duplicate samples of 7 to 8 kg. of fruit of typical size from each plot. Fruits harvested 145 days from bloom were used, as these were considered to be of optimum maturity. Measurements were made for a 24-hour period at intervals of approximately 2 weeks throughout the storage period. Values given for the carbon dioxide output represent in each case the average of determinations on duplicate lots of fruit.

PRESENTATION OF RESULTS

GROWTH RATE

Water deficits in the dry plots as compared with those in the wet were indicated when the rate of fruit enlargement in the dry plot remained definitely below that in the wet plot. Figure 1 shows that in 1936 water deficits in the dry plots in both soils began about 110 days (July 25 to 31) after full bloom and continued through the harvest period. In 1937 the water deficits in the dry plots commenced about 75 to 90 days (July 5 to 15) after full bloom and continued through the harvest period. The enlargement curves indicate that fruit growth was more adversely affected by water deficits in the sandy loam than in the adobe clay. In 1937 there was practically no enlargement of fruit from mid-August to mid-September in the dry plot on sandy loam.

PERCENTAGE OF DRY MATTER AND FIRMNESS

Each year at harvest the percentage of dry matter in the fruit grown on each type of soil was considerably greater for the dry than for the wet plot (fig. 2). The larger percentage of dry matter was accompanied by a greater firmness of flesh except in the fruit grown on adobe clay in 1936. The differences in percentage of dry matter were then relatively small, the firmness of the fruit from the dry plot decreasing to that of the fruit from the wet plot during the latter part of the harvest period. A rather consistent relation was found between water deficit as indicated by the figures for fruit enlargement (fig. 1) and percentage of dry weight and firmness (fig. 2). The greatest difference in rate of fruit enlargement between wet and dry plots was found in the sandy loam in 1937. As shown in figure 2, the greatest difference in percentage of dry matter and fruit firmness occurred in fruit from the same plots (sandy loam, 1936 and 1937).

QUALITY OF FRUIT AFTER STORAGE

In both seasons the fruit picked 135 days or less after full bloom was not sufficiently mature for best dessert quality, but fruit harvested 145 and 155 days after full bloom ripened with satisfactory quality when withdrawn from cold storage in November. In general, fruit from the dry plots was of firmer texture when ripe and consequently less juicy and mellow than fruit from the wet plots (table 1). The fruit from the dry plots was, however, usually sweeter and more highly flavored than that from the wet plots.

Pears grown on the experimental plots in 1936 ripened normally when withdrawn from cold storage on November 15 and December 20. Fruit of the same lots, however, when withdrawn on March 22, 1937, either failed to soften or softened only slightly and did not develop the characteristically smooth, buttery texture of ripe Bosc fruit. As

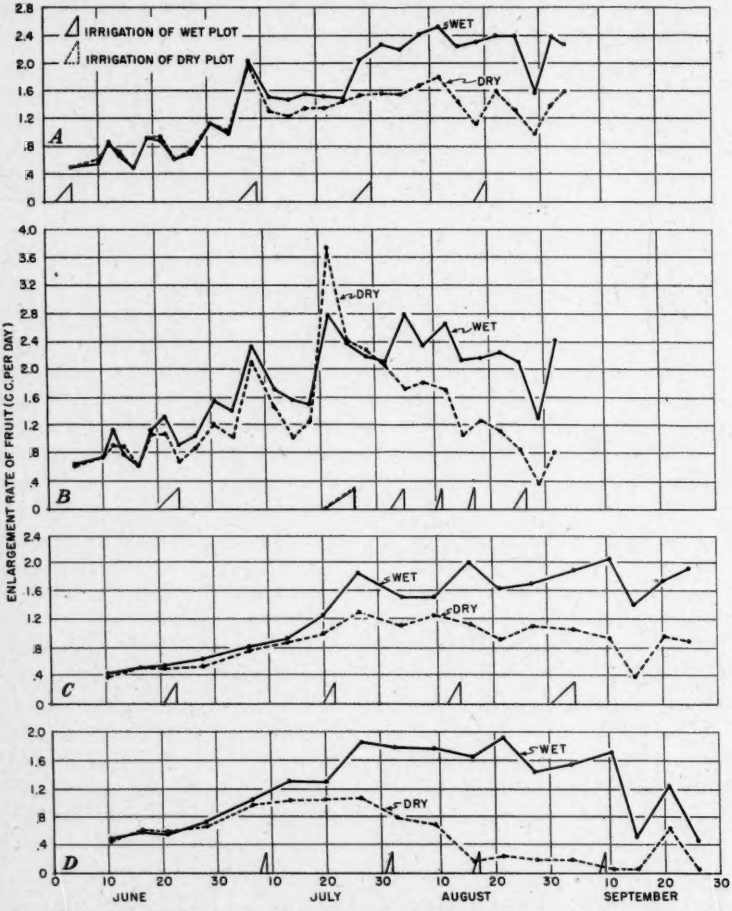

FIGURE 1.—Calculated average daily rate of enlargement of Bosc pears on wet and dry plots: *A*, Adobe clay, 1936; *B*, sandy loam, 1936; *C*, adobe clay, 1937; and *D*, sandy loam, 1937.

shown in table 1, some surface scald appeared on pears from the wet plots in the adobe clay, but none was evident on fruit from the dry plots. This might indicate that senescence was further advanced in the former, but the fact in itself is of little importance, since fruit from both plots failed to ripen normally at this time.

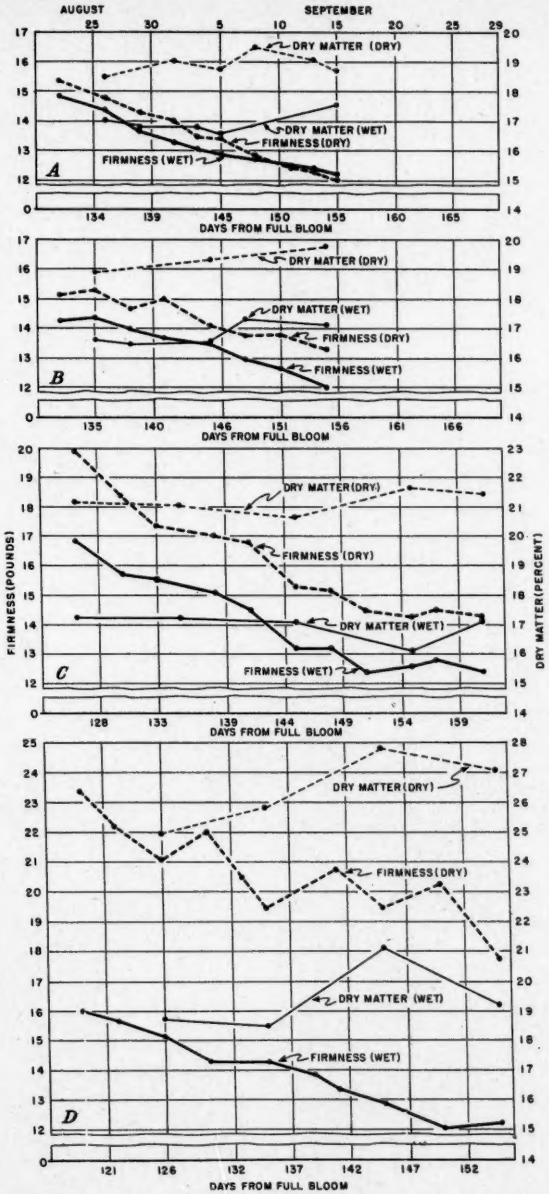

FIGURE 2.—Firmness and dry matter of pears from wet and dry plots: *A*, Adobe clay, 1936; *B*, sandy loam, 1936; *C*, adobe clay, 1937; and *D*, sandy loam, 1937.

TABLE 1.—*Effects of water deficits in the tree upon quality of Bosc pears, 1936 and 1937*

Date of removal from storage and days from bloom to harvest	Kind of plot	Observation at optimum dessert quality when grown on—							
		Adobe clay				Sandy loam			
		Texture	Flavor	Breakdown	Surface scald	Texture	Flavor	Breakdown	Surface scald
Nov. 15, 1936: [1]									
135	Wet	Fairly juicy, smooth	Sweetness lacking	None	None	Fairly juicy, smooth	Sweetness lacking	None	None.
	Dry	do	Fairly sweet	do	do	do	Fairly sweet	do	Do.
145	Wet	Juicy, smooth	Sweet, well flavored	do	do	Juicy, fairly smooth	High flavor lacking	do	Do.
	Dry	Fairly juicy, rather firm	Sweet, highly flavored	do	do	do	Sweet, well flavored	do	Do.
155	Wet	Very juicy, buttery	Very good	do	do	Juicy, smooth	High flavor lacking	do	Do.
	Dry	Juicy, rather firm	do	do	do	Juicy, rather firm	Well flavored	do	Do.
Dec. 20, 1936: [1]									
135	Wet	Fairly juicy, smooth	Sweetness lacking	do	do	Fairly juicy, smooth	Sweetness lacking	do	Do.
	Dry	do	Fairly sweet	do	do	Fairly juicy, firm	Fairly sweet	do	Do.
145	Wet	Juicy, smooth	Sweet, well flavored	do	do	Juicy, fairly smooth	Fair	do	Do.
	Dry	Rather granular	do	do	do	Fairly juicy, rather firm	Sweet, well flavored	do	Do.
155	Wet	Juicy, smooth	Very good	do	do	Juicy, smooth	Flavor lacking	do	Do.
	Dry	Rather granular	Highly flavored	do	do	Rather granular	Well flavored	do	Do.
Mar. 22, 1937: [1]									
135	Wet	Crisp, granular		do	Slight	Some softening, but granular.		do	Do.
	Dry	do		do	None	do		do	Do.
145	Wet	do		do	Moderate	do		do	Do.
	Dry	do		do	None	do		do	Do.
155	Wet	Slight softening, but granular.		do	Slight	Fairly juicy, granular		do	Do.
	Dry	do		do	None	do		do	Do.
Nov. 11, 1937: [2]									
126	Wet	Juicy, fairly smooth	Fairly sweet, lacking flavor.	do	do	Juicy, fairly smooth	Sweetness lacking, astringent.	do	Do.
	Dry	Firm, rather granular	Sweet, fair flavor	do	do	Granular, firm	Fairly sweet, astringent.	do	Do.
135	Wet	Juicy, smooth	do	do	do	Juicy, smooth	Fairly sweet, lacking flavor.	do	Do.
	Dry	Juicy, firm	Sweet, good	do	do	Granular, dry, very firm	Sweet, well flavored	do	Do.
145	Wet	Juicy, smooth	Sweet, well flavored	do	do	Juicy, smooth	do	do	Do.
	Dry	Juicy, firm	Very sweet, highly flavored.	do	do	Granular, firm, dry	do	do	Do.
155	Wet	Fairly juicy, somewhat mealy.	Sweet, well flavored	do	do	Juicy, smooth	Sweet, mild, well flavored.	Slight	Do.
	Dry	Juicy, firm	do	do	do	Granular, firm, dry	Sweet, rather flat	None	Do.

Dec. 11, 1937: [2]									
126	Wet	Mostly crisp, granular	Fairly sweet, poor	do	do	Mostly granular	Poor	do	Do.
	Dry	Firm, crisp, dry	Fair	do	do	Firm, granular, dry	Fair	do	Do.
135	Wet	Mostly crisp, granular	Sweet, fair	do	do	Slightly juicy, crisp	do	do	Do.
	Dry	Firm, crisp, dry	do	do	do	Granular, dry	do	do	Do.
145	Wet	Mostly granular, crisp	Fair	do	do	Some fairly juicy, many granular.	do	do	Do.
	Dry	Firm, dry	Sweet, good	do	do	Granular, dry	Good	do	Do.
155	Wet	Slightly juicy, many crisp.	Sweet, fair	do	do	Some fairly juicy, many granular.	do	Moderate.	Do.
	Dry	Mostly firm, granular	Sweet, good	do	do	Granular, dry	Fair	Slight	Do.

[1] Placed in cold storage Aug. 26, Sept. 5, and Sept. 15, 1936.
[2] Placed in cold storage Aug. 23, Sept. 1, Sept. 11, and Sept. 21, 1937.

As shown in table 1, fruit produced during the 1937 season, regardless of irrigation treatment, failed to ripen normally when withdrawn from cold storage on December 11. No surface scald and only a small amount of break-down were apparent after ripening, but the fruit was largely granular in texture and much of the desirable flavor had been lost.

Regardless of the period the fruit was held in cold storage all appeared to be in good condition when removed to the ripening room. Ripening response in the warm room was the only reliable index of quality after cold storage. Water deficits during the growing season had no effect on the length of the storage life, as judged by ripening response, that could be detected by the three withdrawals from cold storage in the 1936 experiment or by the two withdrawals in the 1937 experiment.

RESPIRATORY ACTIVITY

As shown in figure 3, carbon dioxide production per unit of dry weight of fruit was appreciably greater for fruit from the dry plot than for that from the wet plot. In general, differences between plots were more pronounced in 1937 than in 1936, probably because water deficits in the dry plot were more severe in 1937 than in 1936. Since the fruits from the dry plots were higher in percentage of dry matter than fruits from comparable wet plots, expressing carbon dioxide production in terms of fresh weight instead of dry weight increased the differences shown in figure 3.

CHEMICAL COMPOSITION OF FRUIT

The glucose, fructose, and sucrose present in the fruit at harvest-time are shown in table 2. The percentage of glucose was in all cases lower at the second than at the first picking, but it did not change appreciably after the second picking. Sucrose continued to increase throughout the harvest period, while fructose showed little change.

Fructose and sucrose were consistently lower, when expressed as percentage of dry weight, in fruits from dry than in fruits from comparable wet plots.

On the other hand, there was no significant difference in the percentage of glucose in fruits from the wet and the dry plots. Thus, the ratio of fructose to glucose was lower for the latter.

The decrease in acidity of fruit with advance in maturity during the harvest period, measured both as titratable acidity and as hydrogen-ion concentration (table 3), was not appreciably influenced by water deficits in the summer of 1936.

As shown in table 3, some effect of water deficits upon titratable acidity is indicated in the 1937 season. Since acidity was determined on expressed juice in 1937 rather than on fresh tissue as in the 1936 season, the higher titratable acidity found in fruits from the dry plots in 1937 is probably significant. Fruits from wet and dry plots on sandy loam showed the greatest difference, and, as previously mentioned, the dry plot on sandy loam suffered the greatest water deficits.

The index figures, as shown in table 3, appear to be of little significance, because in most cases the highest index figure did not coincide with the most desirable maturity. In several cases the highest index figure was obtained for fruits of the first picking in 1937, which were distinctly immature.

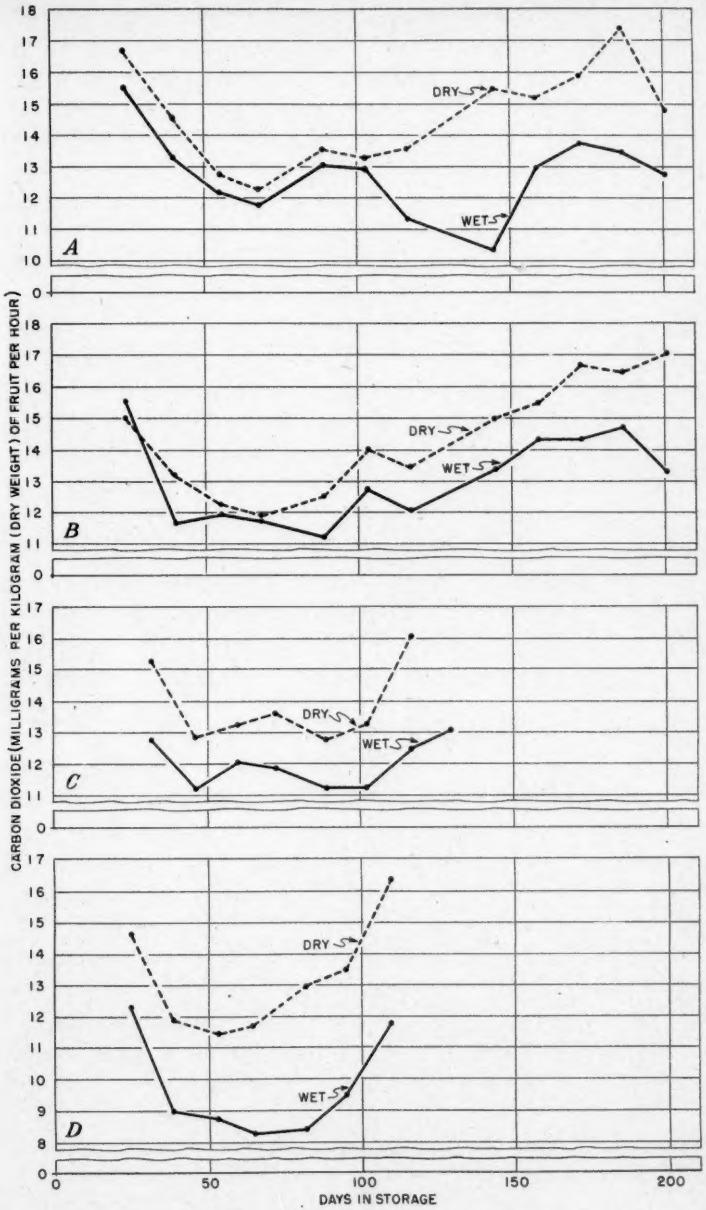

FIGURE 3.—Carbon dioxide output of pears (dry-weight basis) grown on wet and dry plots and stored at 31° F.: *A*, Adobe clay, 1936; *B*, sandy loam, 1936; *C*, adobe clay, 1937; and *D*, sandy loam, 1937.

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TABLE 2.—*Effects of water deficits in the tree upon carbohydrate content of Bosc pears, 1936 and 1937*

Kind of soil and date of harvest	Period from bloom to harvest	Wet plot						Dry plot					
		Fresh-weight basis			Dry-weight basis			Fresh-weight basis			Dry-weight basis		
		Glucose	Fructose	Sucrose (as invert)	Glucose	Fructose	Sucrose (as invert)	Glucose	Fructose	Sucrose (as invert)	Glucose	Fructose	Sucrose (as invert)
Adobe clay:													
1936	*Days*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
Aug. 26	135	1.60	3.31	2.28	9.39	19.44	13.33	1.55	3.86	1.88	8.37	20.84	10.10
Sept. 5	145	1.10	4.23	2.62	6.63	25.50	15.79	1.25	4.24	2.25	6.67	22.61	11.95
15	155	1.10	4.23	3.48	6.27	24.10	19.83	1.33	3.99	3.41	7.12	21.36	18.23
1937													
Aug. 23	126	1.35	3.41	1.52	7.83	19.80	8.82	1.69	3.38	1.54	8.00	16.00	7.28
Sept. 1	135	1.10	3.55	2.25	6.38	20.60	13.02	1.21	3.66	2.30	5.75	17.38	10.92
11	145	1.05	3.89	3.03	6.15	22.80	17.17	1.07	3.83	3.36	5.17	18.48	16.16
21	155	1.22	3.99	3.06	7.57	24.77	19.03	1.27	3.76	3.50	5.87	13.37	16.18
Sandy loam:													
1936													
Aug. 25	135	1.65	3.57	1.61	9.91	21.44	9.67	1.82	3.69	1.49	9.62	19.51	7.89
Sept. 4	145	1.22	3.96	2.18	7.36	23.88	13.15	1.55	3.81	2.39	8.01	19.69	12.35
14	155	1.36	3.68	2.63	7.94	21.48	15.35	1.69	3.37	2.96	8.53	17.00	14.93
1937													
Aug. 30	126	1.47	3.91	1.84	7.85	20.89	9.77	2.06	3.19	2.29	8.25	12.77	9.12
Sept. 8	135	1.14	3.87	2.42	6.16	20.92	13.08	1.80	3.35	2.92	6.96	12.95	11.28
18	145	1.33	3.85	3.37	6.28	18.19	15.92	1.93	3.47	3.60	6.92	12.44	12.88
28	155	1.16	3.61	3.83	6.03	18.75	19.90	1.82	3.12	4.07	6.69	11.48	14.99

TABLE 3.—*Effect of water deficits in the tree upon titratable acidity and hydrogen-ion concentration of Bosc pears, 1936 and 1937*

Kind of soil and date of harvest	Period from bloom to harvest	Wet plot			Dry plot		
		N/10 NaOH	pH	Index figure	N/10 NaOH	pH	Index figure
Adobe clay:							
1936	*Days*	*Ml.*		10^{-7}	*Ml.*		10^{-7}
Aug. 26	135	[1] 7.5	4.16	19.2	[1] 7.7	4.27	14.3
Sept. 5	145	[1] 7.3	4.30	14.4	[1] 6.8	4.32	14.3
15	155	[1] 6.1	4.40	13.5	[1] 5.9	4.45	12.3
1937							
Aug. 23	126	[2] 10.6	4.23	13.9	[2] 12.5	4.32	9.6
Sept. 1	135	[2] 8.5	4.40	11.7	[2] 10.2	4.44	8.9
11	145	[2] 9.0	4.38	11.6	[2] 9.2	4.49	8.8
21	155	[2] 8.5	4.45	10.4	[2] 8.7	4.56	7.9
Sandy loam:							
1936							
Aug. 25	135	[1] 8.5	4.40	9.7	[1] 8.3	4.42	9.3
Sept. 4	145	[1] 7.5	4.33	13.0	[1] 7.1	4.38	11.8
14	155	[1] 6.8	4.38	12.7	[1] 7.1	4.42	10.8
1937							
Aug. 30	126	[2] 10.7	4.23	13.8	[2] 13.0	4.43	7.1
Sept. 8	135	[2] 7.7	4.47	11.0	[2] 10.0	4.43	9.3
18	145	[2] 7.2	4.52	10.5	[2] 8.7	4.78	4.8
28	155	[2] 7.5	4.45	11.8	[2] 8.7	4.74	5.2

[1] To neutralize 25 gm. of fresh tissue.
[2] To neutralize 25 ml. of expressed juice.

DISCUSSION

In view of the relative severity of the water deficits in the trees on the dry as compared with those on the wet plots, particularly in 1937, it is not surprising that the water deficits so markedly affected the percentage of dry matter, firmness, sugar content, and carbon dioxide output of the fruit. The increased percentage of dry matter and the greater firmness of the fruit experiencing severe water deficits may have been largely or entirely the result of the reduced water content of the fruit. It is probable that a reduced supply of carbohydrates in trees suffering appreciable water deficits accounted for the lower fructose, sucrose, and total-sugar content of the fruit from the dry plots as compared with that of the fruit from the wet plots, on the basis of percentage dry weight. These effects of water deficits in the late summer in decreasing the percentage of total sugars per unit of dry weight are in agreement with those reported for Anjou pears (*1*) and are consistent with the findings of Schneider and Childers (*7*), who reported reductions in the apparent photosynthesis in apple leaves with a limitation in soil moisture.

The fact that the carbon dioxide output of fruit from the dry plots was greater than that of fruit from the wet plots was probably due in part to the smaller size of fruit from the dry plots and the resultant greater number of fruits per unit of weight. As fruit growth on the dry plots was almost the same as that on the wet plots during April, May, and June, the period of cell division in the fruits, it is probable that the smaller size of fruits on the dry plots after June was largely the result of smaller cells rather than of fewer cells. Thus it is perhaps reasonable to assume that the fruit from the dry plot had more cells per unit weight and that this was responsible for the greater metabolic activity per unit weight indicated for fruit from the dry plots. The greater surface area of the fruit from the dry plots per unit of weight may also have been a factor in the greater output of carbon dioxide.

The fact that greater respiratory activity per unit of dry weight in the fruit from the dry plots resulted in no measurable shortening of the storage life as compared with that from the wet plots is consistent with the findings of Gerhardt and Ezell (*3*), who reported no direct correlation between the respiratory activity of winter pears and the length of storage life at 32° F.

The effects of water deficits on firmness of the fruit, as measured by the pressure tester, are important inasmuch as this measurement is one of the principal indexes of maturity. Since the fruit from the dry trees was consistently much firmer than fruit from the normally irrigated (wet) trees, it is apparent that the accepted range of firmness for harvest would not be a trustworthy index for fruit from trees with appreciable water deficits. Ripening tests indicated that, in spite of greater firmness, fruit from the dry plots was as mature as fruit from the wet plots at the same number of days from bloom.

The surprising result is that these effects of severe water deficits were not accompanied by a greater influence upon the quality of the fruit when withdrawn from cold storage and ripened. The extremely severe water deficits in the dry trees in sandy loam in 1937 did result in fruit which ripened with granular, firm flesh rather than with the normal, smooth, buttery texture. This was apparently due, however,

to the exceptionally low water content of the fruit rather than to the loss of ripening response. As a result of water deficits this fruit was too small to meet even the minimum commercial requirements; so such lack of quality would not be expected in commercially packed fruit. Apparently, when the water deficits in the tree during the summer are not sufficiently severe to prevent the fruit's reaching commercially acceptable sizes, such water deficits would be expected to be of only minor importance in influencing the storage or dessert quality of Bosc pears.

There was no evidence that Bosc fruits grown on fine-textured soils had better storage qualities than those grown on coarse-textured soils. There was some indication, however, that Bosc fruits grown on the adobe clay were slightly more desirable from the standpoint of flavor and texture than those grown on sandy loam. The wide difference in fruit quality frequently observed in different years was also manifest in the results of these 2 years.

SUMMARY

Bosc pears from trees given moderate and light applications of water were harvested for determination of the effects of water deficit upon the fruit.

Water deficits in the trees on the dry plots were indicated by a consistently reduced rate of fruit growth as compared with that of fruits on the comparable wet plots. Such water deficits began about 75 to 110 days after full bloom and continued through the harvest period.

Percentage of dry matter, determined on the freshly harvested fruits, was higher in fruits from the dry plots than in those from the wet plots. Frequently, when the firmness of fruits from the dry plots was several pounds above the accepted range for picking, the pears were actually mature, as judged by quality when subsequently ripened. Thus, where appreciable water deficits in the trees occur, firmness standards developed for fruit from adequately irrigated trees may not be satisfactory indexes of maturity.

Pickings for storage and quality determinations were made at certain intervals after full bloom, the intervals ranging from 126 to 155 days.

Ripened pears from the wet plots were usually somewhat smoother and mellower in texture, but only in the case of very severe water deficits was the texture of pears from the dry plots unacceptable.

Pears from the dry plots were noticeably sweeter when ripened than those from the wet plots. Pears from the wet plots, however, when ripened early in the season and of proper maturity were sufficiently sweet and well flavored to be readily acceptable to the consumer.

Carbon dioxide output at 31° F., as shown by milligrams of carbon dioxide per kilogram (dry weight) hour, was consistently greater for fruit grown on the dry plots, and the difference was related to the severity of the deficit.

Fructose, sucrose, and total sugars, when calculated on a dry-weight basis, were in general higher in pears grown on wet plots than in those grown on dry plots. Percentage of glucose, calculated on dry weight, was not materially affected by water deficits in the trees.

Titratable acidity and hydrogen-ion concentration were usually somewhat higher in the expressed juice of pears from the dry plots than in that of pears from the wet plots.

There was no indication that water deficits during the growing season affected the storage life of Bosc pears.

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THE AMPHIDIPLOIDS AEGILOPS CYLINDRICA × TRITICUM DURUM AND A. VENTRICOSA × T. DURUM AND THEIR HYBRIDS WITH T. AESTIVUM [1]

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INTRODUCTION

It is generally recognized that the 21 pairs of chromosomes found in the cells of common wheat, *Triticum aestivum* L. (*T. vulgare* Vill.),[2] comprise 3 different sets of 7 pairs each. One of these sets, designated A, is homologous to the 7 pairs of chromosomes that make up the entire complement of *T. monococcum* L. ($n=7$). This is shown by the occurrence of 7 pairs (and 14 unpaired chromosomes) at meiosis in hybrids between *T. aestivum* and *T. monococcum*. Similarly, the 14 chromosome pairs of the emmer wheats ($n=14$), such as *T. dicoccum* Schrank and *T. durum* Desf., are known to be homologous to sets A and B of *T. aestivum*. The third or C set (called D by Japanese workers) does not occur in any wheat with fewer than 21 pairs of chromosomes, but it has been found in *Aegilops cylindrica* Host ($n=14$), a wild relative. Its occurrence in *A. cylindrica* has been detected through observations of chromosome association in hybrids of that species with emmer and *T. aestivum* wheats. In hybrids with the emmers, Bleier (*1*) [3] and others have found usually no pairing between the *Aegilops* and *Triticum* chromosomes; whereas in hybrids with the *T. aestivum* wheats, several investigators, including Sax and Sax (*13*), have usually observed 7 pairs. By producing from *A. cylindrica* and *T. durum* an amphidiploid hybrid containing the full complement of chromosomes from both parents, and then crossing this amphidiploid with *T. aestivum*, it has now been possible to make a more direct test for the presence of the C set of chromosomes in *A. cylindrica*.

Aegilops ventricosa Tausch ($n=14$) resembles *A. cylindrica* in the pairing behavior of the chromosomes in its hybrids with emmer wheats

[1] Received for publication February 10, 1943. These studies are a part of the program supported by funds obtained under the Bankhead-Jones Project S. R. F.-2-5, "Comparative Genetics and Cytology of Polyploid Series in *Triticum*." Cooperative investigations of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, and the Field Crops Department, Missouri Agricultural Experiment Station. Contribution from the Field Crops Department, Missouri Agricultural Experiment Station, Journal Series No. 863.

[2] *Triticum aestivum*, originally applied by Linnaeus to the bearded spring wheats only, under the International Rules of Botanical Nomenclature becomes the specific name for all common bread wheats, since it was the earliest name applied to any of the varieties of this group. The concept of this species as emended by Host under the name of *T. vulgare* Vill. is that now most generally accepted by wheat specialists. Wheat specialists likewise have preferred the name *T. vulgare* because it is more truly descriptive of the species. The name *T. vulgare*, however, is untenable under present rules of nomenclature, since it was originally proposed by Villars merely to replace the earlier name, *T. aestivum*. It is hoped, however, that at an appropriate time the rules can be amended so that the name *T. vulgare* can be conserved for this species.

[3] Italic numbers in parentheses refer to Literature Cited, p. 143.

(*5, 9, 11*) and has shown up to seven or more pairs of chromosomes in hybrids with *A. cylindrica* (*4, 11*). It has given no viable hybrids with *T. aestivum*, but Kihara and Lilienfeld (*7*) have concluded from crosses of it with other species of *Aegilops* having $n=14$ that it does not possess the C set. This conclusion has now been tested directly, through cytological study of a hybrid between *T. aestivum* and the amphidiploid *A. ventricosa* × *T. durum*.

MATERIAL AND METHODS

Three varieties of *Triticum durum* were used in making the hybrids from which the amphidiploids were produced. For crossing with *Aegilops ventricosa*, a variety (apparently Mindum) obtained from the Minnesota Agricultural Experiment Station was employed. In the *A. cylindrica* crosses both Acme and F. P. I. No. 94587 [4] were used.

Two forms of *A. cylindrica*, one glabrous and one pubescent, were used in the crosses. Both are referable to *cylindrica* var. *pauciaristata* Eig.

A. ventricosa was all of one type, var. *comosa* (Coss.) Eig.

Two varieties of *T. aestivum*, Chinese and Hope, were used for crossing with the amphidiploids.

For the production of amphidiploids from F_1 material, colchicine treatments as previously described (*14*) were used. Since untreated plants of *Aegilops ventricosa*×*Triticum durum* set numerous seeds, somatically doubled sectors could not be identified with certainty in this hybrid, and no conclusions could be drawn concerning the efficiency of the various methods of treatment. With *A. cylindrica*×*T. durum*, the best results were obtained by applying a 0.5-percent aqueous solution of colchicine to cotton-packed crowns of potted plants for a period of 4 days. Treatments of crowns of potted plants with 0.4 percent of colchicine in lanolin for 4 days, or of shoots of very young, unplanted seedlings (with coleoptiles 5 to 10 mm. long) with 0.1 or 0.2 percent of colchicine in lanolin for 1 day, were less successful. A treatment of seedlings with 0.4 percent of colchicine in lanolin was lethal to all 11 individuals to which it was applied.

Cytological observations were made for the most part from fresh acetocarmine smears of material fixed about 2 days in Carnoy's solution. The smears were prepared as described previously (*15*), except that anthers were frequently fixed singly in order to provide clearer division figures, as recommended by Love (*8*). Some studies were made from smears made permanent either by the tertiary butyl alcohol technique previously described (*15*) or by the following improved method:[5]

1. Soak off cover slip in 1 part glacial acetic acid to 1 part tertiary butyl alcohol. The cover slip may have to be loosened with a needle if drying has occurred around its edges.
2. Transfer slide and cover slip to pure tertiary butyl alcohol for a few minutes.
3. Add a drop of balsam and replace the cover slip.

The advantages of this method are that immersion oil and sealing material are dissolved by the tertiary butyl alcohol and no destaining occurs in preparations left overnight or longer in either of the fluids.

[4] Accession number of the Division of Plant Exploration and Introduction, Bureau of Plant Industry, Soils, and Agricultural Engineering.

[5] Developed in collaboration with Dr. Herschel Roman.

HYBRIDS AND AMPHIDIPLOIDS

AEGILOPS CYLINDRICA × TRITICUM DURUM

The hybrid *Aegilops cylindrica* × *Triticum durum* and its amphidiploid derivative were intermediate between the two parent species in many characteristics of the spike (fig. 1) and other plant parts.

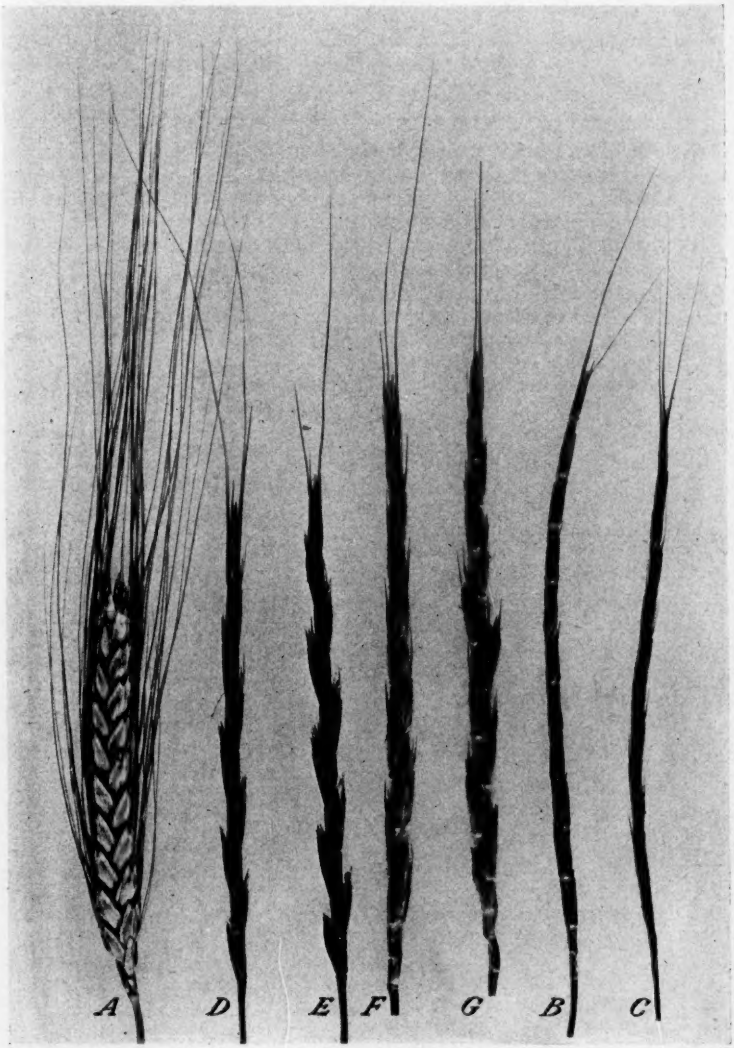

FIGURE 1.—Mature spikes of (*A*) *Triticum durum*, (*B*, *C*) *Aegilops cylindrica* (glabrous and pubescent, respectively), and (*D*–*G*) their F_1 hybrids. Glabrous *A. cylindrica* was involved in *D* and *E*, and pubescent in *F* and *G*. Spikes *D* and *F* are 2*n*; *E* and *G*, 4*n*. ×¾.

Little difference was observed between 4*n* (doubled) and 2*n* (nondoubled) portions of the same F_1 plant.

TABLE 1.—*Chromosome pairing at first metaphase in F_1 hybrids*

Hybrid	Microsporocytes examined	Univalents per cell		Bivalents per cell		Cells with univalents only
		Range	Average	Range	Average	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Aegilops cylindrica × *Triticum durum*	100	22–28	27.00	0–3	0.50	66
Aegilops ventricosa × *Triticum durum*	100	20–28	27.64	0–4	.18	87

Meiotic chromosome pairing in the nondoubled hybrid (table 1) was similar to that reported by other investigators. Most microsporocytes had only univalents at first metaphase, and the bivalents present had only a single, usually terminal chiasma.

Untreated F_1 plants set no seeds. The anthers, which did not dehisce, usually contained over 99 percent of aborted pollen.

The amphidiploid showed a high frequency of univalents at meiosis (table 2), 3.6 per microsporocyte in the most regular plant studied. Multivalent associations were infrequent.

TABLE 2.—*Chromosome pairing at first metaphase in amphidiploids*

Amphidiploid	Microsporocytes examined	Univalents per cell		Cells with no univalents
		Range	Average	
	Number	*Number*	*Number*	*Number*
Aegilops cylindrica × *Triticum durum*	50	0–12	3.60	4
Aegilops ventricosa × *Triticum durum*	50	0–10	2.56	13

The fertility of the amphidiploid was rather low, the seed set being less than 20 percent, even on the most fertile 56-chromosome plant. The most fertile spike had only 64 percent of seed set, and no other had as much as 50 percent. About 75 to 80 percent of the pollen was normal in appearance.

Chromosome numbers among the offspring of amphidiploid plants were predominantly abnormal, as is shown in table 3. Only 6 out

TABLE 3.—*Chromosome numbers in offspring of amphidiploid plants*

Amphidiploid	Season	Plants grown	Plants examined	Plants with indicated number of chromosomes					
				52	53	54	55	56	57
		Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Aegilops cylindrica × *Triticum durum*	1941	18	10	1	2	-------	3	3	1
	1942	12	12	-------	-------	-------	7	3	2
Aegilops ventricosa × *Triticum durum*	1940	8	5	-------	1	1	2	1	-------

of the 22 plants classified had 56 chromosomes, and the true frequency of perfectly normal plants may have been even lower. In both the 1941 material, which was grown from seeds on colchicine-treated

plants, and the 1942 material, which came from seeds on two 56-chromosome individuals in the 1941 planting, some of the plants with 56 chromosomes may have had 1 or more monosomes plus an equal number of trisomes. Such abnormalities could have been overlooked in the poorly synapsed metaphases. In the 1941 material, furthermore, only the earliest and most vigorous individuals were examined cytologically, and these were probably the plants that were most nearly normal in chromosome constitution. This possible selection in the 1941 material was offset, however, by the further possibility that some of the seeds used were of nonamphidiploid origin on the female side. Such seeds, produced in 2*n* florets of partly 4*n* spikes, would presumably have tended particularly toward abnormal chromosome constitution, because of their origin through the formation of restitution nuclei rather than through the normal meiotic process.

AEGILOPS VENTRICOSA × TRITICUM DURUM

The hybrid *Aegilops ventricosa* × *Triticum durum* and its amphidiploid derivative resembled the *A. cylindrica* × *T. durum* hybrid in being morphologically intermediate between the parent species (fig. 2), in having little 2*n*-chromosome pairing (table 1), and in showing a high frequency of univalents in the amphidiploid (table 2). In 2*n* fertility, however, the *ventricosa-durum* hybrid was distinctly higher. Sufficient good pollen (probably between 10 and 25 percent) was present to bring about dehiscence of anthers, and numerous seeds were set from self-pollination. Since the two hybrids were grown in different years, the higher fertility of the 2*n* *ventricosa-durum* material may have been partly an environmental effect, as is suggested by the fact that an F_1 plant of *A. ventricosa* × *T. durum* grown in the same year as the *cylindrica-durum* material set no seeds. However, this hybrid plant involved a different variety of *T. durum* (F. P. I. No. 94587) from that represented in previous *ventricosa-durum* hybrids. Furthermore, Sorokina (*16*) observed 0.21 percent of seed set in *A. ventricosa* × *T. durum* hybrids.

In amphidiploid fertility, also, *ventricosa-durum* was higher than *cylindrica-durum*. Several spikes had over 90 percent of seed set, and the entire 56-chromosome plant probably averaged well over 50-percent fertility. Pollen was about 75 to 80 percent normal in appearance.

Of the 5 offspring of colchicine-treated plants examined cytologically (table 3), only 1 had 56 chromosomes. This frequency is similar to that observed in the progeny of *cylindrica-durum* amphidiploids, but there is more reason to suspect that some or all of the *ventricosa-durum* seeds came from nondoubled florets through restituted male as well as female gametes. Although the seeds for planting were selected from the most fertile spikes, there is little assurance that these spikes were entirely 4*n*. Some fairly fertile spikes were found also on untreated plants.

Of 7 plants grown from seeds on untreated material, 2 had 55 chromosomes, 3 had 54 chromosomes, 1 had 51 chromosomes, and 1 was not studied. Sorokina (*16*) also obtained some apparently amphidiploid offspring from untreated F_1 plants of *Aegilops ventricosa* × *Triticum durum*, but did not study them cytologically.

FIGURE 2.—Mature spikes of (*A*) *Aegilops ventricosa*, (*B*) *Triticum durum*, and (*C*) their amphidiploid hybrid. ×⅔.

HYBRIDS OF AMPHIDIPLOIDS WITH TRITICUM AESTIVUM

AEGILOPS CYLINDRICA-TRITICUM DURUM × T. AESTIVUM

The cross *Aegilops cylindrica-Triticum durum* × *T. aestivum* was made between a 56-chromosome amphidiploid plant and the variety Chinese of *T. aestivum*. The seed set was comparable to that in the open-pollinated amphidiploid, and of the 8 hybrid seeds tested all were viable. Thirteen seeds of the reciprocal combination were all

inviable. Of the 8 plants grown, 4 were examined cytologically and were found to have the following chromosome numbers: 46, 47, 49, and 49. Only the latter 2 will be considered further.

Studies of chromosome relationships in the hybrids were hampered by the scarcity of analyzable division figures. Some microsporocytes were found, however, which definitely had 21 pairs and 7 univalents (fig. 3). This pairing must represent the association of the A and B sets of *Triticum aestivum* with the chromosomes of *T. durum*, and the association of the C set of *T. aestivum* with 7 of the 14 chromosomes of *A. cylindrica*. The intensity of pairing and the absence of heteromorphic bivalents in cells like the one shown in figure 3 indicated fairly complete homology between the *T. aestivum* C set and 1 *A. cylindrica* set. Trivalents and other multivalents were rare, giving little indication that chromosomes of the second *A. cylindrica* set have much affinity for any of the chromosomes of *T. aestivum*.

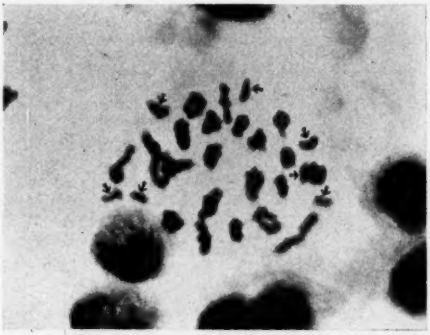

FIGURE 3.—First metaphase in a microsporocyte of (*4n Aegilops cylindrica* × *Triticum durum*) × *T. aestivum*, showing 21 bivalents, 7 univalents. Univalents are indicated by arrows. × 670.

Fertility was low in the amphidiploid-*aestivum* hybrid. Of the two plants available, one had nondehiscent anthers and set no seed and the other had dehiscent anthers containing approximately 25 percent of normal pollen and set four seeds following open pollination (presumably selfing) in the greenhouse. The pollen was functional on both the amphidiploid and *Triticum aestivum*, about one seed per spike being obtained.

TRITICUM AESTIVUM × AEGILOPS VENTRICOSA-T. DURUM

The varieties Chinese and Hope of *Triticum aestivum* were crossed with colchicine-treated F_1 plants of *ventricosa-durum*. Of 9 hybrid seeds involving Chinese, 5 grew; 3 of the resulting plants had 48 chromosomes, and 2 had 47. Of 4 Hope × amphidiploid seeds, 3 grew, and the 2 resulting plants that were examined cytologically had 47 and 49 chromosomes, respectively. All further cytological data were obtained from the 49-chromosome plant.

From 4 to 13 univalents per microsporocyte were observed, averaging 8.7, in 28 cells. If there were no homology between the C set of chromosomes of *Triticum aestivum* and the chromosomes of *Aegilops ventricosa*, 21 univalents would be expected in this hybrid; while com-

plete homology between the C set and 7 chromosomes of *A. ventricosa* would leave 7 chromosomes unpaired. The average occurrence of only 8.7 univalents shows that a considerable amount of homology exists. This homology is imperfect, however, for, besides there being usually more than 7 univalents, frequent trivalents and quadrivalents occurred. No microsporocyte with exactly 21 pairs and 7 univalents was found. It seems likely that only homoeology (i. e., homology involving 1 or more regions of 2 chromosomes but not their entire length) exists between the C chromosomes of *T. aestivum* and the chromosomes of *A. ventricosa*, and that some of the C chromosomes are homoeologous to 2 or more *ventricosa* chromosomes.

Fertility was considerably higher in this hybrid than in *Aegilops cylindrica-Triticum durum* × *T. aestivum*. One open-pollinated (presumably selfed) spike had 9 seeds, a set of about 35 percent. The whole 49-chromosome plant probably averaged close to 10 percent of seed set. Even the plants with 47 and 48 chromosomes set some seeds.

DISCUSSION

The results reported here provide direct confirmation of the assumption that *Aegilops cylindrica* possesses the C chromosome set of *Triticum aestivum*. They also confirm the conclusion of Kihara and Lilienfeld (7) that the intact C set is not present in *A. ventricosa*, although the data indicate considerable homoeology between the C set and *ventricosa* chromosomes.

Meiosis in the amphidiploids was characterized by a general reduction in chiasma frequency, usually with the occurrence of univalents. Loss or irregular distribution of these univalents was presumably the chief cause of the low fertility observed. Since these are intergeneric hybrids, their abnormal meiotic behavior might be attributed to incompatibility of the 2 diverse genoms. However, various other amphidiploid hybrids between species of *Triticum* and *Aegilops* have little or no tendency toward asynapsis. Four synaptic amphidiploids with $n=14$ have been reported by the writer (*15*), and 1 more is now available in this group (*A. bicornis* (Forsk.) Jaub. and Spach × *T. monococcum*). Also of good synaptic behavior are amphidiploids of *T. dicoccoides* Körn. ($n=14$) with *A. caudata* L. ($n=7$), *A. sharonensis* Eig ($n=7$), *A. speltoides* Tausch ($n=7$), and *A. umbellulata* Zhuk. ($n=7$), although *T. dicoccoides* × *A. comosa* Sibth. and Smith ($n=7$) had considerable asynapsis.[6] There is reason to doubt, therefore, that incompatibility of diverse genoms is responsible for the poor pairing in the *cylindrica-durum* and *ventricosa-durum* amphidiploids. It seems more probable that the large number of chromosomes hinders pairing in some way. All other 56-chromosome wheat amphidiploids reported have tended to have univalents at meiosis and to be of reduced fertility: *A. ovata* × *T. dicoccoides* (*6, 17*), *A. ovata* × *T. durum* (*17*), *A. ovata* × *T. turgidum* (*12*), and *T. aestivum* × *Secale cereale* (*10*).

Of the hybrids of the two amphidiploids with *Triticum aestivum*, the one involving *ventricosa-durum* was distinctly the more fertile, in spite of its less regular meiosis. It had a frequency of univalents substantially the same as did the hybrid involving *cylindrica-durum*, and had multivalent configurations as well. There is some reason to suspect,

[6] Unpublished data.

however, that it had more regular pairing of members of the A and B sets of chromosomes with their homologues, since somewhat better pairing occurs in the *ventricosa-durum* amphidiploid than in *cylindrica-durum*. This greater regularity of A and B pairing would result in a higher proportion of *aestivum* × *ventricosa-durum* gametes with a full complement of A and B chromosomes. Evidence from other hybrids indicates that the possession of complete sets of both A and B chromosomes is ordinarily essential for gametic viability.

Further interest is attached to these amphidiploids because of their possible practical value. Much improvement in *Triticum aestivum*, particularly with respect to disease resistance, has been attained through hybridization with *T. durum* and *T. dicoccum*. No use has ever been made of *Aegilops cylindrica* and its C chromosome set, however, although Johnston (*2*) and Jones (*3*) have shown that *A. cylindrica* is highly resistant to leaf rust and hessian fly. If the resistance factors lie in the C set of *cylindrica* chromosomes, it should be possible, by means of relatively simple crossing and selection procedures, to transfer part or all of the resistance of the *cylindrica-durum* amphidiploid to *T. aestivum*.

The *ventricosa-durum* amphidiploid may also be of practical value, since Jones found that *Aegilops ventricosa* also is resistant to hessian fly. Although no perfect homologues of the *Triticum aestivum* C chromosomes exist in *A. ventricosa*, the resistance factors may be transferable to C chromosomes through homoeologous pairing and crossing over.

SUMMARY

By treating hybrids of *Aegilops cylindrica* × *Triticum durum* and *A. ventricosa* × *T. durum* with colchicine, amphidiploid sectors were obtained. In addition, *A. ventricosa* × *T. durum* produced a number of seeds on untreated plants.

Chromosome pairing in the amphidiploids was poor and fertility was low, particularly in *cylindrica-durum*. Aneuploid chromosome numbers predominated among the offspring.

Hybrids of the amphidiploids with *Triticum aestivum* (*T. vulgare*) confirmed the previous assumption that *A. cylindrica*, but not *A. ventricosa*, possesses homologues of the C set of *T. aestivum* chromosomes. Considerable homoeology was indicated, however, between *A. ventricosa* chromosomes and the *T. aestivum* C set.

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